

The somatosensory system is organized in a hierarchy of populations of neurons<sup>1</sup>. The neurons in the subcortical and primary somatosensory cortex (S1) are topographically arranged at each point in the hierarchy such that neurons that are adjacent (more or less) selectively respond to stimuli in adjacent regions of the body. It has been found that the somatosensory cortex is plastic, in the sense that regions that used to respond selectively to mechanical stimulation of a particular digit can come to respond selectively to mechanical stimulation of an adjacent digit if that first digit is removed<sup>2</sup>. It has also been found that mechanically stimulating a particular digit or digits repeatedly can result in cortical magnification of the region/s processing that information.

The motor system is similarly arranged in hierarchical populations of neurons. There is a topographic arrangement here, too, with adjacent neurons resulting in movement or muscular contraction of (more or less) adjacent regions of the body. The representational contents of the motor cortex (M1) seem to have been the subject of much more controversy than the representational contents of the sensory cortices, however (at least that is the impression that I got from the textbook especially regarding visual processing)<sup>3</sup>. We need to have some idea of what the neurons in M1 represent order to assess whether the representational contents of those neurons have changed or whether they are likely to be able to change in a way that is comparable to the plasticity that has been found in S1.

Most of the controversy over the contents of M1 seems to be over whether the neurons represent *movement* or whether they represent *contraction of muscles*. There seems to be evidence for both where stimulating single neurons results in muscular contraction, whereas stimulating a region of adjacent neurons results in movements such as grasping or grimacing. One concern with regarding individual neurons to code for muscular contraction was that the tuning curves of individual neurons in M1 were fairly coarse grained with respect to their selectively (or not very selectively) being activated prior to a range of different movements. It was unclear to me whether the different movements involved an overlap of muscular contraction that corresponded to the overlap of individual neuronal activation, however. If this were found to be the case then the coarse grained tuning curve in relation to movement wouldn't be evidence against individual neurons having a more refined tuning curve in relation to muscular contraction.

In favor of M1 neurons coding for movement it was found that direction of movement could be predicted from averaging the activity of the neuronal population and that direction of arm movement, in particular, could be predictably altered by temporarily anesthetizing a subregion. The direction of movement wasn't able to be predicted from the activity of individual neurons, however, as the tuning curves are too coarse with respect to movement, as we have seen. I would be interested to know whether the monkeys were able to correct their direction of movement over a number of trials in the face of temporary anesthetizing a subregion of M1. If so, then this would seem to be an interesting case of behavioral / movement plasticity as a function of (temporary) damage and training where the representational content of the anesthetized region is presumably replicated (or compensated for) in some way by the surrounding region.

<sup>1</sup>As are the other sensory systems. I'll focus on the somatosensory system here, however.

<sup>2</sup>I will restrict myself to the issue of plasticity in the central nervous system of adult primates.

<sup>3</sup>I've been struggling with the a-symmetry between the sensory and motor systems where sensory systems representational contents are given by the contents of the systems that are temporally prior (typical causes), but where motor systems representational contents are thought to be given by the contents of systems that are temporally later (typical effects). We can predict the contents of the visual system fairly well with respect to retina, LGN, and V1. I'd be interested to know whether we are able to retrodict the contents of the visual system comparably well with respect to V1, LGN, retina. If so, then the a-symmetry probably doesn't matter. If not, then I'm simply not sure whether or not this is an important a-symmetry that will have further ramifications (e.g., for plasticity or for multiple realizability of representational contents) or not.

Perhaps the disagreement over the representational contents of M1 can be sorted if people are clear about whether they are talking about the representational contents of individual neurons in M1, or whether they are talking about the representational content of the population (or of some sub-population) of neurons in M1. With respect to what the neurons in M1 are *really* coding for, that might turn out to be about as interesting as whether an ambiguous figure is *really* a duck or *really* a rabbit (which is to say not at all)<sup>4</sup>. It might be that whether one is interested in how M1 is tuned to either muscular contraction or movement determines whether one is (or should be) more interested in individual neurons or the population of neurons. I really don't see why this isn't a similar issue / problem (or perhaps non-problem) for the contents of sensory systems (including the visual system).

The relationship between individual tuning curves and population tuning curves is going to be complex. The population is going to supervene on the individuals. That is to say that there cannot be a change in the (tuning curve) properties of a population without a change in the (tuning curve) properties of the individuals that comprise the population<sup>5</sup>. The population is also going to be multiply realizable. That is to say that there can be a change in the (tuning curve) properties of the individuals that comprise the population without a change in the (tuning curve) properties of the population<sup>6</sup>. Some cognitive neuroscientists (e.g., Bechtel) deny multiple realizability. Still, it does seem that motor programs may be multiply realized by movements and that movements may be multiply realized by muscular contractions. Multiple realizability together with supervenience (which seems fairly obviously to apply to compositional relations such as populations and the individuals that comprise them as well as to muscular contractions, movements, and motor programs) together seem to imply that there will be more plasticity at the ontology of lower levels than at the ontology of higher levels, however. Despite this, it seems fairly obvious that motor programs such as signing ones name or pressing a lever are very plastic on the basis of behavioral evidence that they can be acquired in adulthood. It would thus be highly surprising to me if movements weren't found to be plastic (my argument requires them to be even more so). Whether the plasticity is similar to that of the sensory system remains to be seen.

The issue then becomes one of what constraints there may be on plasticity. While motor programs may be massively multiply realizable with respect to muscular contractions, movement will be multiply realizable, though less so. Topography might well limit the tuning curves of individual neurons with respect to the connections they bear to inputs (in the case of sensory systems) and outputs (in the case of the motor system). If we grant that transducers and lower motor neurons are non-plastic in the sense that lower motor neurons don't attach themselves to different muscles even if the connections to fibers within a muscle may vary, then it might be that there are different degrees of plasticity at different levels of the processing (or individual / sub-population / population) hierarchy. Still, my argument bothers me because it seems to imply that individuals (or low level processing) will be more plastic than population (or higher level) processing. Something other than the motor system seems to be backwards (or maybe upside down). Still, I did read that individual neuron tuning curves vary over time, anyway. It may be that it is easier to fire with proximal rather than distal relations and that the plasticity of individual neurons in particular is constrained by what ones relatives are doing.

<sup>4</sup>Though it could be that I'm missing some of the significance of the data, here.

<sup>5</sup>Gaining or losing members counts as a change in the individuals.

<sup>6</sup>Supervenience and multiple realizability are also thought to be features of the software / hardware distinction and are likely features of the relationship between muscular contraction, movement, and motor program responses. Both of these relations are a-symmetric, which gets me worrying about a-symmetry between the sensory and motor systems, again. On a slightly different note I'm used to a similar distinction between sensory, perceptual, and *conceptual* representational contents. I didn't appreciate that they were going to be lumped together until Cowan. If I had have appreciated it in the perception unit I would have had much to say about it...