The connection from cortical area V2 to V5 in macaque monkey.
John C Anderson and Kevan A C Martin.
Institute for Neuroinformatics, University of Zurich and ETH Zurich, Winterthurerstr. 190, Zurich, Switzerland.

Introduction
The interconnections between cortical areas have been extensively explored. This information has been used to develop models of circuits and connectivity. Projecting pathways have been shown to be different between different areas and depending upon the lamina location of neurons and their terminals have been described as feed forward or feedback. Area V5 or MT has been described as the so-called “motion area”. The projection to V5 from V1 has an extensive history of investigation. We have previously studied the terminals of V1 axons in V5 and can now make a comparison with the projection of the secondary visual area V2.

Methods
Cortical area V2 of two rhesus monkeys was micro-injected with Phaseolus vulgaris Leucoagglutinin (Pha-L). Injection sites were from 1 - 2 mm in diameter. After a survival period of 14 days the animals were anaesthetised and perfused with a solution of para-formaldehyde (4%), gluteraldehyde (0.3%) and picric acid (15%) in saline. Tissue from areas V1 and V5 was sunk in sucrose (10-30%) and vibratome sectioned. The PhaL was visualised by a Vector ABC kit and DAB histology. Portions of labeled axon and boutons were selected in the light microscope (LM) for serial ultrathin sectioning and subsequent electron microscopic (EM) examination. Complete boutons, their synapses and targets were reconstructed from electron micrographs. We used the physical disector method to estimate the number of labeled boutons in area V5.

Results
The major target of the V2 projection from V5 is layer 4 with a few boutons in layers 1 and 2. Spines were the most frequent target, 67% and 82% in layers 4 and 2/3. Boutons formed on average 1.1 synapse/bouton. In the densest areas of innervation in layer 4 V2 boutons contributed 4-6% of asymmetric synapses.

Figure 1
Schematic drawing of macaque brain showing region in which injections were made (between dots) along the edge of the lunate sulcus, near the V1/V2 border (dotted line).

Figure 2
Light micrograph of cortical area V5 showing PhaL labeled axons and boutons. A, Patchy distribution of labeled terminals in layer 4. B, Adjacent section to A, higher magnification. Complete boutons, their synapses and targets were reconstructed from electron micrographs. We used the physical disector method to estimate the number of labeled boutons in area V5.

Figure 3
Electron micrographs of PhaL labeled boutons in layer 4 of area V5, asymmetric synapses are indicated (arrowheads). A, Two boutons form synapses with spine heads (sp, green). B, Bouton forms synapse and puncta (small arrow) with a dendritic shaft (d, yellow) that also forms symmetric synapse (open arrow) with unidentified bouton. Scale: 0.5μm.

Figure 4
Histogram of the synaptic targets of labeled V2 boutons in V5.

Figure 5
Histogram of the number of synapses formed by labeled V2 boutons in layers 2/3 and 4 of area V5.

Figure 6
Histogram of the distributions of diameters of labeled V1 and V2 axons near the border between white matter and layer 6 of area V5. All measurements were made in the LM.

Figure 7
Summary
As with the V1 projection the V2 terminals are primarily located in layer 4 of V5 where they form clusters of asymmetric (excitatory) synapses. The V2 projection also extends throughout the superficial laminae into layer 1. The most frequent synaptic targets were spines and most boutons formed only one synapse. Both V1 and V2 boutons in V5 form synapses of similar size. The clear differences between the V1 and V2 projection to V5 indicate that their functions are complimentary rather than completely overlapping.

Supported by: SNSF, HFSP, EU.