

## Corollary discharge and spatial updating: when the brain is split, is space still unified?

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**Abstract:** How does the brain keep track of salient locations in the visual world when the eyes move? In parietal, frontal and extrastriate cortex, and in the superior colliculus, neurons update or 'remap' stimulus representations in conjunction with eye movements. This updating reflects a transfer of visual information, from neurons that encode a salient location before the saccade, to neurons that encode the location after the saccade. Copies of the oculomotor command — corollary discharge signals — must initiate this transfer.

We investigated the circuitry that supports spatial updating in the primate brain. Our central hypothesis was that the forebrain commissures provide the primary route for remapping spatial locations across visual hemifields, from one cortical hemisphere to the other. Further, we hypothesized that these commissures provide the primary route for communicating corollary discharge signals from one hemisphere to the other. We tested these hypotheses using the double-step task and subsequent physiological recording in two split-brain monkeys. In the double-step task, monkeys made sequential saccades to two briefly presented targets, T1 and T2. In the visual version of the task, the representation of T2 was updated either within the same hemifield ("visual-within"), or across hemifields ("visual-across"). In the motor version, updating of the visual stimulus was always within-hemifield. The corollary discharge signal that *initiated* the updating, however, was generated either within the same hemisphere ("motor-within") or in the opposite hemisphere ("motor-across"). We expected that, in the absence of the forebrain commissures, both visual-across and motor-across conditions would be impaired relative to their "within" controls.

In behavioral experiments, we observed striking initial impairments in the monkeys' ability to update stimuli across visual hemifields. Surprisingly, however, both animals were ultimately capable of performing the visual-across sequences of the double-step task. In subsequent physiological experiments, we found that neurons in lateral intraparietal cortex (LIP) can remap stimuli across visual hemifields, albeit with a reduction in the strength of remapping activity. These behavioral and neural findings indicate that the transfer of visual information is compromised, but by no means abolished, in the absence of the forebrain commissures. We found minimal evidence of impairment of the motor-across condition. Both monkeys readily performed the motor-across sequences of the double-step task, and LIP neurons were robustly active when within-hemifield updating was initiated by a saccade into the opposite hemifield. These results indicate that corollary discharge signals are available bilaterally. Altogether, our findings show that both visual and corollary discharge signals from opposite hemispheres can converge to update spatial representations in the absence of the forebrain commissures. These investigations provide new evidence that a unified and stable representation of visual space is supported by a redundant circuit, comprised of cortical as well as subcortical pathways, with a remarkable capacity for reorganization.

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