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Multisensory maps in parietal cortex☆

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Parietal cortex has long been known to be a site of sensorimotor integration. Recent findings in humans have shown that it is divided up into a number of small areas somewhat specialized for eye movements, reaching, and hand movements, but also face-related movements (avoidance, eating), lower body movements, and movements coordinating multiple body parts. The majority of these areas contain rough sensory (receptotopic) maps, including a substantial multisensory representation of the lower body and lower visual field immediately medial to face VIP. There is strong evidence for retinotopic remapping in LIP and face-centered remapping in VIP, and weaker evidence for hand-centered remapping. The larger size of the functionally distinct inferior parietal default mode network in humans compared to monkeys results in a superior and medial displacement of middle parietal areas (e.g., the saccade-related LIP's). Multisensory superior parietal areas located anterior to the angular gyrus such as AIP and VIP are less medially displaced relative to macaque monkeys, so that human LIP paradoxically ends up medial to human VIP.

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Unisensory versus multisensory

The shortest path between any pair of neurons in the brain often involves just few intervening synapses. For example, in mice, primary visual cortex projects directly to entorhinal cortex [1••]; similarly, in primates, parietal visual areas project directly, if sparsely, to V1 [2,3••]. Thus, in some sense, every brain area is potentially a 'multisensory' area [4,5].

But taking primate V1 as an example, single-unit spikes there are most strongly modulated by the presence of simple visual features (orientation, direction of movement) in the classical excitatory receptive field, or by large arrays of similar low-level visual features in the non-classical surround. Simple auditory, vestibular, and somatosensory stimuli have small effects on the spiking of primate V1 neurons, though they can more strongly modulate the size or latency of subthreshold membrane potentials, and consequently EEG/MEG or fMRI signals. By contrast, spiking activity in neurons in an explicitly multisensory area, such as primate ventral parietal area (VIP) and rodent rostrolateral area (RL), is typically strongly modulated by both visual and somatosensory stimuli applied to localized regions of the receptor sheets, either individually or in combination.

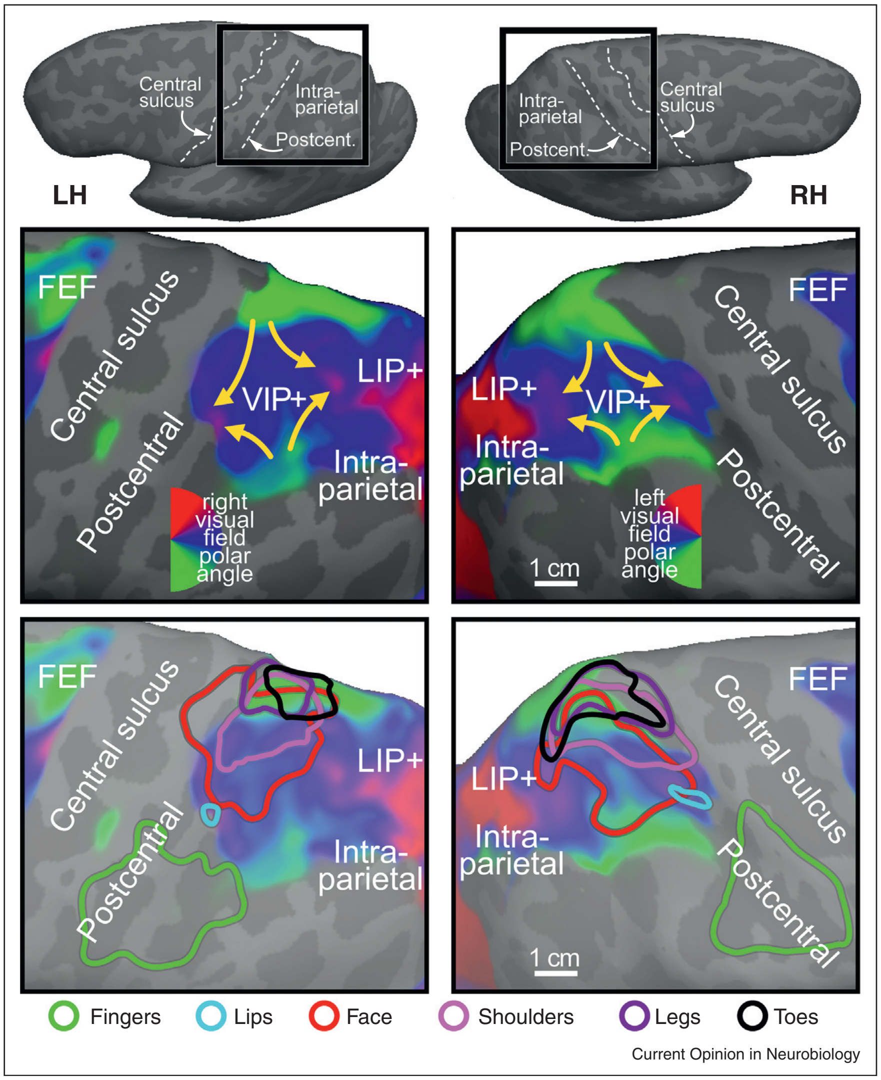
Another consideration is that species differ in the overall depth of their visual cortical area hierarchies. For example, in small nocturnal mammals that have less well developed visual capabilities, like mice, V1 neurons are more strongly modulated by the behavioral context of stimuli (e.g., see [6]); in primates, there are more intervening synapses from motor cortex to V1 [1••,3••], which might explain why primate V1 is more strictly visual at the level of single units. This review concentrates on mapping overtly multisensory areas in parietal cortex (for previous reviews, see [7–9,10••,11]).

Ventral intraparietal area (VIP) — the parietal face area

VIP was originally defined in macaque monkeys as a visual area containing neurons with large visual receptive fields that also had aligned somatosensory receptive fields on the face and shoulders [12]. More recent experiments have suggested that VIP might instead be thought of as a somatosensory area focused on operations in face-centered space that also has visual input. Avoidance and defensive motor responses from stimulating VIP [10••,13] and a preference for stereoscopic stimuli near the face [14] suggest that one primary function is to protect the face.

In humans, a multisensory area containing somatotopic maps of air-puff stimuli to the face superimposed and aligned with retinotopic maps of up-close visual stimuli was found in the postcentral sulcus, just posterior and slightly medial to the S-I hand representation [15,16] in a region originally identified as multisensory by Bremmer *et al.* [17]. This region is also activated during paradigms as diverse as mental arithmetic [18] and delayed reaches in complete darkness toward extinguished visual targets [19], and so it is likely to be involved in many cognitive functions involving actions

Figure 1



Overlapping retinotopic (upper panel) and somatotopic (lower panel) maps in human anterior parietal cortex. The upper row close-ups show 24-subject average polar angle maps from wide-field direct-view fMRI mapping using a moving video wedge (complex-valued surface-based spherical coordinate system averaging method described in [56]). Four lower → middle → upper field traverses are visible in VIP+ in each hemisphere (yellow arrows). The color contours in the lower row show spherically aligned somatotopic whole body mapping data from [24••] (face data [15]) over the grayed visual data (body part key is at bottom). Top insets show the location of the magnified views on the unfolded, dorsolaterally tilted cortex.

or events in real or metaphorical peripersonal space. For example, when we say 'the holidays are approaching', we treat the holidays as if they were looming objects (compare the syntactically equivalent 'the children are approaching') [20]. One of the overlaid functions of multisensory parietal areas in humans may be to generate or interpret the meaning of such utterances.

Recent fMRI evidence in macaque monkeys has demonstrated that face somatosensory inputs and visual inputs overlap in one or more localized regions of the fundus of the intraparietal sulcus rather than extending along its entire length [21]. This result is compatible with human mapping studies, which have uncovered multiple, somewhat variable, overlapped representations of the face and retina [15]. Surface-based cross-subject average retinotopic maps suggest that the population average pattern in the anterior most part of visual parietal cortex consists of two separated (anterior and posterior) upper field representations and two separated (medial and lateral) lower field representations (see Figure 1, upper). This results in four lower-to-upper visual field progressions. Multiple aligned representations of the face overlay a portion of these visual maps (see red contours in Figure 1, lower).

The parietal body area (greater VIP)

Electrical stimulation studies in parietal cortex of several different non-human primates using the 'extended