

Multisensory integration: **Attending to seen and felt hands**

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The neglect of one side of space exhibited by some brain-damaged patients can be ameliorated by cueing the patient to the neglected side of space. A related effect has been found to depend on the hand being seen and felt at the same time. The results add to a growing literature on somatosensory–visual interactions.

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Most of the excellent work on single-unit neurophysiology has focussed on stimulus-related activity in a single input modality, such as vision or audition. Other work has also been modality-specific, but has involved studying, not sensory inputs, but motor outputs, directed at understanding how neurons in the motor cortex fire in relation to different parameters, such as movement direction or velocity. More recently, neurophysiologists have turned their attention to the question of how multiple effectors, such as the eyes and hands, are coordinated with one another. Similarly, a new generation of studies have shown how more than one sensory modality can influence the activity of single neurons in the superior temporal, parietal and frontal neocortex of primates.

Some of the most fascinating of these latter studies have been conducted by Charles Gross, who described multimodal neurons of the temporal lobes some 30 years ago, and Michael Graziano at Princeton. They were the first to provide detailed reports on single neurons — first found subcortically in the putamen [1], later in premotor cortex [2] — that have bimodal receptive field properties: their firing rates are ‘turned on’ by both visual and somatosensory stimuli. The sensory properties of these units — their so-called ‘receptive fields’, referring to the areas of skin or the visual world where stimulation produces the largest changes in their firing patterns — are matched for spatial location. That is, a cell which responds preferentially to tactile stimulation on a certain part of the face will have a visual receptive field in ‘peripersonal’ space near to, and aligned with, that somatosensory receptive field (Figure 1).

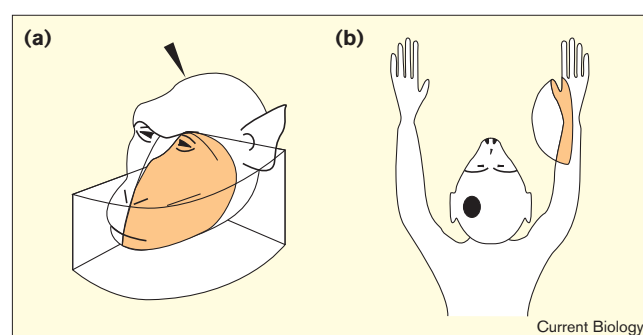
The receptive fields of these prefrontal bimodal cells have another remarkable characteristic: they move with the body part. In the case of neurons which respond to tactile

stimulation on the arm (Figure 1b), the visual receptive fields move with the arm and not with the eye, as do many visual receptive fields in other parts of the central nervous system (CNS). In much the same fashion, the visual field of a facial tactile neuron (Figure 1a) will move with a head turn, but not with a turn of the eyes while the head remains stationary (for reviews of these incredible neurons, see [1,3]).

These findings have helped to inspire a number of fascinating experiments (or at least their interpretations) on patients with various attentional and somatosensory disorders. For example, Rorden *et al.* [4] looked at how a patient’s expectancies about somatosensory and visual stimulation coming from the same source influenced the ability to detect touch in a patient with poor somatosensory processing in an arm after a cerebral lesion. In one condition, the patient was required to detect taps of his unseen hand when a small light-emitting diode was flashed on the table surface above it, on the finger of the hand of the experimenter. On some trials, the flashes coincided with taps of the unseen hand, on other trials they did not. Performance on these trials was poor. But when the experimenter’s hand was replaced by a rubber hand with the diode placed on it, in approximately the same orientation and position as the unseen hand below the table, the patients performance was dramatically improved.

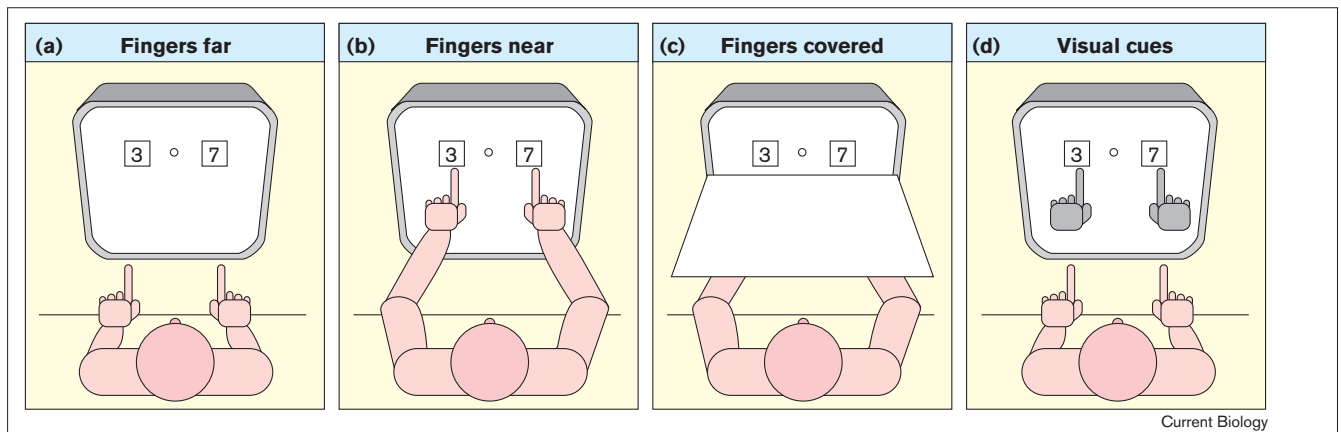
The ‘congruence’ of the seen rubber hand and the unseen hand was somehow established by the subject’s brain,

Figure 1



Bimodal cells with spatially congruent receptive fields. In (a), the visual receptive field of a face neuron (outlined) is restricted to peripersonal space immediately around the tactile receptive field (orange shading). The visual receptive field of this type of cell is yoked to the head. In (b), the visual receptive field of an arm neuron is indicated by the outlined area and the tactile receptive field with orange shading. The visual receptive field of such neurons are yoked to the arm. (Adapted from [12].)

Figure 2



The experimental conditions in di Pellegrino and Frassinetti's study [6]. In the conditions illustrated in (a,c,d), the patient often did not see the number flashed to the left of a fixation point on a computer screen.

When his hands were placed near the two target locations (b), his ability to identify the left-sided targets improved dramatically. (Modified from [6].)

producing performance remarkably improved over the condition where the visual flash was on the experimenter's hand. The mismatch of the seen experimenter's arm and the unseen patient's arm is reminiscent of our own study [5], which required participants to look at an afterimage of their own hand in complete darkness and then generate a movement. In one condition, we found that afterimages of a left hand were never erroneously mapped onto a subsequently moving right hand [5].

A similar phenomenon has now been described by di Pellegrino and Frassinetti [6], in a paper published recently in *Current Biology*. They have demonstrated improvements in attention to bilateral visual stimulation that are apparently caused by a mechanism that 'binds' somatosensory and visual stimuli in peripersonal space. Their patient, DP, had suffered a lesion to the right side of his brain, and when a stimulus was presented in his affected, left visual hemifield he failed to detect it — but only when it was presented at the same time as a different stimulus was shown on the right, unaffected side. This is a mild form of a well-known phenomenon known as 'extinction'.

Next, di Pellegrino and Frassinetti [6] found that DP's ability to detect the left-sided visual target was much improved if he placed his two hands near the computer screen, the left hand near the location where the left target would appear and the right hand near where the right target appears (Figure 2b). This recovery could be explained by some sort of sensory cueing — drawing attention to the extinguished left side by presenting another stimulus in that space. This phenomena is well described in the literature on hemispatial neglect (see for example [7]) as well as that on extinction (for example [8]).

In this case where the hands provide possible cues, it could have been that the proprioceptive stimulus of the left arm cues attention to the left target location. After all, the extinction in the patient was visual, not somatosensory. Not so — covering the hands with the card brought the extinction back to the level of when the hands were distant from the target locations (Figure 2c). Perhaps the sight of the left hand cued the patient to attend to left target locations? After all, the hand is quite a large visual stimulus relative to the letter targets, and the patient had no visual field defects. Not so — when a visual cue of the same size and shape of the hand was provided at the same location, extinction occurred just like that seen when the hands were distant in the control condition (Figure 2d). These data must mean that felt and seen hands *both had to be present* for the extinction to disappear.

These data are fascinating in their own right, but they can also be useful for interpreting some recent results in cognitive psychology on 'supramodal' models of attention. For example, Spence and colleagues [9] found that participants were best at detecting visual and tactile targets when they were attending to one side of space for both modalities. The authors interpret their data as indicating that "crossmodal attentional links should operate within more abstract spatial coordinates" rather than "fixed anatomical mappings" [9]. In other words, even if your right hand (monitored by somatosensory cortex of the left hemisphere) is across the body midline in the left visual hemifield (monitored by right hemisphere visual cortices), these stimuli seem bound together by attentional processes. The results of di Pellegrino and Frassinetti [6] and Graziano and colleagues [3] come to mind here. The attentional fields around somatosensory stimuli of significance like hands

move when the hands move [2], even if they cross the body midline.

Some important outstanding questions remain in the domain of somatosensory–visual integration. For example, note in the case of di Pellegrino and Frassinetti's [6] patient DP, for extinction to be eliminated both the visual and the somatosensory stimuli had to be in the 'right' place — the vicinity of the left hand. But what if the two stimuli really had to be in register? That is, not just near the left-sided target on the computer screen, but right 'on top' of one another? Most of the bimodal receptive fields described in the monkey central nervous system were of the 'either–or' variety: they would fire to a visual stimulus in the right place or a somatosensory one in the right place. One wonders where populations of such cells send their information to? In other words, where in the CNS do we find truly bimodal cells, which fire only in response on simultaneous exposure to the stimuli from different sensory modalities with similar (or the same) positions in three-dimensional space?

Many questions remain unexplored by these intriguing studies into cross-modal integration. Are these bimodal binding mechanisms very smart or very sloppy? Our own study [5] suggests that, for afterimages of a hand to be mapped onto an unseen hand in complete darkness, the register between the seen and felt stimulus has to be quite tight in three dimensions (for example, on the appropriate place on the retina as well as in the right place in depth). But evidence that some of the mechanisms are quite 'spatially tolerant' has come from several fascinating mislocalisation illusions (for example, [10,11]). For example, if the arm of a participant is hidden from view, and a mannequin's arm is placed in close register, it is possible to stroke the unseen arm with a paintbrush while simultaneously stroking the mannequin arm. In spite of the spatial mismatch between seen and felt limbs — not to mention some obvious 'top-down' processing — participants are astounded to find that they 'feel' the stroking motions of the seen paintbrush on the arm of the mannequin [11].

Michael Graziano [3] has replicated this finding with single unit recording in monkey premotor cortex. In these experiments, however, rather than using a mannequin, unfortunate conspecifics of the participants became acquainted with a local taxidermist — at least part of them did — as real (stuffed monkey arms) were used. Covering the arm of the monkey reduced the responsiveness of bimodal neurons to approaching visual stimuli. The similarity of this finding to the behavioural results reported by di Pellegrino and Frassinetti [6] was not lost on the latter scientists. I am intrigued by the final finding in Graziano's study [3]: placing the stuffed monkey arm above the covered arm in full view of the animal caused substantial, though not complete, recovery of the vigorous

responses to approaching stimuli when the monkey could 'see' its felt arm.

A final area worthy of some interest by the clever scientists working in this area is the plasticity of these bimodal systems. For example, if a mismatch between seen and felt limb positions is produced by wearing glasses containing displacing prisms, participants quickly 'recalibrate'. I wonder if the tolerance for slight spatial mismatches ('slop') in bimodal cells in the brain is somehow related to these fast, efficient recalibrations. Although producing somatosensory displacements is perhaps not as easy as slapping on a pair of prism spectacles, there is surely some scope for tendon vibration experiments in this domain. In the meantime, I eagerly await the prism adaptation studies on patients with bimodal extinction phenomena, as well as on single cells of the premotor cortex of non-human primates not yet familiar with the taxidermist.

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