Crossmodal Integration: A Glimpse into the Development of Sensory Remapping

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Correctly localising sensory stimuli in space is a formidable challenge for the newborn brain. A new study provides a first glimpse into how human brain mechanisms for sensory remapping develop in the first year of life.

Newborn infants receive a wealth of information about the world from many different senses. Some of these are distal senses such as vision, and others, like touch, are experienced through the body. In some instances, it is sufficient to use a body frame of reference to localize a touch on our skin, for example, when perceiving that a fly has landed on our hand. However, when acting on external events — for example, reaching out to swat the fly — the nervous system needs to combine distal and body-based sources of somatosensory information. Neural recordings show that, in newborn cats and rhesus monkeys [1,2], some such crossmodal mappings develop soon after birth, and that early sensory experience is crucial for shaping multisensory processing. What is unclear however, is how and when humans develop the ability to align multiple sensory maps of space. A study by Rigato *et al.* [3] reported in this issue of *Current Biology* provides important new insights into the early development of human neural mechanisms that map touches on the body to external locations in space.

In human adults, automatic mapping of tactile inputs to their locations in external frames of reference is evident in a disadvantage for judging which hand was touched first when the hands are crossed [4]. This is because, in this situation, somatosensory maps in anatomical coordinates become misaligned with those in external coordinates. In adults, this behavioural index of spatial remapping is also reflected in early modulation by hand-crossing of event-related electro-encephalogram (EEG) potentials over the somatosensory cortex [5]. Somatosensory evoked potentials (SEPs) therefore provide an index of humans' automatic remapping of touch to take limb position into account. Rigato *et al.* [3] recognised the potential of the hand-crossing paradigm for examining somatosensory remapping in 6-month-old and 10-month-old infants. In their study, infants experienced vibration on their hands in crossed and uncrossed positions, and SEPs were recorded via electrodes on the scalp. When 6-month-old infants crossed their hands, SEPs were similar to those when the hands were uncrossed, indicating no remapping of body representations into external space. By 10

months, however, SEPs were reduced when hands were crossed compared to when they were uncrossed. This effect was already evident at early latencies, indicating that fast, automatic remapping of body position into external space occurred at this age [5].

This finding is supported by an earlier behavioural study with infants, in which Bremner and colleagues [6] showed that it was only at 10 months that infants correctly oriented and reached towards touches when the hands were crossed. In contrast, 6-month-old infants experiencing crossed-hand stimulation responded towards the side on which the hand would normally be. The new EEG study[3] builds upon these previous findings by also revealing that the cortical signal related to remapping was only present in 10-month-old infants when they were able to see their hands. This stands in marked contrast to adults, who can also remap using proprioceptive joint-position information alone[4]. This shifting balance between proprioception and vision for touch perception reveals how cross-modal mechanisms for somatosensory remapping can change radically in human development. This is in line with recent evidence that sensory interactions involving vision, proprioception and touch undergo major development long into childhood [7–9].

Besides providing a first glimpse into how somatosensory remapping mechanisms develop, the work by Rigato *et al.* [3] raises important new questions about the changes in neural processing underlying this development. These early changes may reflect the maturation of brain areas that represent or combine different types of cross-modal representations. Alternatively or additionally, they may reflect the development of connectivity between brain areas. During the first year of life, connectivity across remote areas in the brain increases dramatically [2,10]. The corpus callosum, one of the major structures connecting the two hemispheres, increases substantially in thickness and size [11]. Corpus callosum function appears to be crucial for somatosensory remapping, as shown by Spence *et al.* [12] in a study revealing an absence of remapping effects in an adult 'split-

brain' patient with a sectioned corpus callosum. This led Spence *et al.* [12] to conclude that in adults, the registration of visuotactile space with postural changes crucially relies on bimodal cells in cortical structures, such as ventral premotor cortex and parietal cortex, and cannot solely be supported by subcortical structures, such as the putamen and superior colliculus.

Since the Spence *et al.* [12] study, the human cortical networks at play during somatosensory mapping have been unraveled in much more detail [13]. Disruption by transcranial magnetic stimulation (TMS) of processing in hVIP, a putative human homolog of monkey area VIP in the intraparietal sulcus [14], impairs judgments of relative limb position [13], showing this area's involvement in remapping of touch into an external frame of reference. Area hVIP receives non-visual information about arm position and skin-based touch percepts from area 5 in superior parietal cortex, and is thought to integrate this information with visual information about body posture from other intraparietal sulcus regions [13,15,16]. Thus, the emergence of remapping at around 10 months of age might be closely linked to improved interhemispheric communication, or might reflect maturation of cortical areas involved in somatosensory integration across different frames of reference.

But while the earlier-mentioned patient and TMS studies [12,13] revealed that cortical areas are necessary for somatosensory remapping in adults, this need not necessarily be the case in infants. That is, early remapping could rely more on subcortical bimodal neurons and then shift towards a stronger reliance on cortical representations later in life. Thus, while Rigato *et al.* [3] clearly show that remapping of touch into external frames of references first emerges in infants during the first year of life, this by no means implies that the processes underlying this ability are adult-like by this age. Indeed, even at 6 years of age, judgments of which hand was touched first are less impaired by crossing the hands than they are at later ages [17]. This indicates that the mechanisms involved in somatosensory remapping continue to be fine-tuned for many years after infancy.

Another question raised by the work of Rigato *et al.* [3] is what kinds of experience are required for the development of cross-modal remapping abilities. The present finding of infants' early reliance on vision is in line with evidence for remapping in late-onset blind (12 years and older) but not in congenitally blind individuals [18]. In animal models, multisensory spatial maps do not develop normally in absence of vision [1], and congenitally blind children are also impaired in purely *tactile* judgments of orientation [19]. Why is early vision so important? One possibility is that the major other route to judging limb position, proprioception, is unreliable in young infants. This might particularly be the case early on, when body representations need to change rapidly because of rapid growth of the body. Alternatively, it may be that vision uniquely provides the rich spatial information needed to learn to relate body-based reference frames to representations of the external world.

The body postures and actions of very young infants are very limited, so immature remapping abilities in early infancy would have little practical consequence. However, motor abilities improve rapidly during the first year of life [20]. This introduces a need for continuous updating of body representations with external representations across vastly different body postures. It is conceivable that such motor experience not only occurs in sync with the emergence of remapping abilities, but also plays a functional role in their development. Consistent with this possibility, Rigato *et al.* [3] report that among 8-month-olds, only a sub-group who (in a separate behavioural study) showed spontaneous hand-crossing when reaching for objects also showed a significant difference in crossed vs uncrossed SEPs.

The new findings [3] provide a first glimpse into how brain mechanisms for remapping sensory stimuli in space emerge in the first year of life. Major questions raised include what brain changes underlie the SEP results, and how these changes are shaped by specific kinds of visual or motor experience. Understanding the effects of experience [18,19]

on neural remapping mechanisms will have important applications for atypical development. Reorganisation of sensory mapping in infancy [3,6] implies that this may be a period of great developmental vulnerability. However, it may also be the period in which therapeutic interventions to restore sensory function can have the most far-reaching effects. For example, providing a treatment for sight loss in the first year of life may have a major impact not only on visual development, but also on the development of normal somatosensory processing.

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