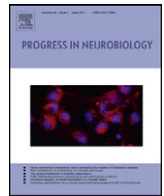




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The human somatosensory system: From perception to decision making

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ABSTRACT

Pioneering human and animal research has yielded a better understanding of the brain networks involved in somatosensory perception and decision making. New methodical achievements in combination with computational formalization allow research questions to be addressed which increasingly reflect not only the complex sensory demands of real environments, but also the cognitive ones.

Here, we review the latest research on somatosensory perception and decision making with a special focus on the recruitment of supplementary brain networks which are dependent on the situation-associated sensory and cognitive demands. We also refer to literature on sensory-motor integration processes during visual decision making to delineate the complexity and dynamics of how sensory information is relayed to the motor output system.

Finally, we review the latest literature which provides novel evidence that other everyday life situations, such as semantic decision making or social interactions, appear to depend on tactile experiences; suggesting that the sense of touch, being the first sense to develop ontogenetically, may essentially support later development of other conceptual knowledge.

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Abbreviations: ACC, anterior cingulate cortex; A1, primary auditory cortex; BA, brodmann area; BOLD, blood-oxygen-level-dependent; DLPFC, dorsolateral prefrontal cortex; DCM, dynamic causal modeling; EMG, electromyography; EEG, electroencephalography; ERP, event-related potentials; FEF, frontal eye fields; fMRI, functional magnetic resonance imaging; IFG, inferior frontal gyrus; IPL, inferior parietal lobe; IPS, intraparietal cortex; LIP, lateral intraparietal area; M1, primary motor cortex; MedFG, medial frontal gyrus; MFG, middle frontal gyrus; MLE, maximum likelihood estimation; MT, motion area; MEG, magnetoencephalography; OFC, orbitofrontal cortex; PET, positron emission tomography; PMC, premotor cortex; rTMS, repetitive transcranial magnetic stimulation; SI/1, primary somatosensory cortex; SII/2, secondary somatosensory cortex; SMA, supplementary motor area; SFG, superior frontal gyrus; SPL, superior parietal lobe; VMPFC, ventral medial prefrontal cortex.

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1. From sensory input to perception and perceptual decision making

Sensory input from inside or outside the body is transmitted via peripheral nerves to the central nervous system. When it reaches the brain it may become a conscious experience, depending on the stimulus's characteristics and the state of the sensory system. Conscious experience or “perception” of sensory inputs enables decisions to be made based on them, as well as further cognitive processing of them. To this end, the brain needs to evaluate stimuli, especially with respect to their relevance for potential actions.

In this review, we focus on the neurobiological mechanisms of perception and perceptual decision making in the somatosensory system. In the first part, we provide evidence concerning the cortical processing of somatosensory stimuli below and above threshold, as well as the states of the somatosensory system which influence the likelihood of conscious perception. In the main section, we will discuss cerebral models and respective evidence of how sensory inputs are utilized for perceptual decision making. Furthermore, we spotlight new research topics which aim to explore the way touch influences non-tactile impressions and decisions, such as semantic decisions and social interactions.

2. Somatosensory perception

2.1. Electroencephalography for the identification of sensory and cognitive brain generators

Although tactile perception and decision making are still not well understood, the interest in related somatosensory brain responses reaches back to the 70s. In many electroencephalography (EEG) studies, event-related potentials (ERPs) were recorded from the scalp during serial selective tactile tasks. The aim was to distinguish components of the ERPs with respect to their distinct sensory and cognitive brain generators.

Today, it is well known from functional magnetic resonance imaging (fMRI)-based brain imaging studies, that tactile or electrical stimulation of the fingers is associated with evoked activity in the contralateral primary cortex (SI) and the bilateral secondary somatosensory cortex (SII), as well as in the superior and inferior parietal lobule, the supplementary and cingulate motor area, and the insula (see e.g., Ruben et al., 2001; for location of SI and SII activation see Fig. 1).

Before the establishment of fMRI techniques, researchers mainly used EEG to investigate sensory, as well as cognitive, generators, mainly with respect to their role in the processing of visual and auditory stimuli. Besides early ERP components known

to consistently reflect early sensory processing, responses occurring late after stimulus presentation, such as the P300, were discussed in relation to categorization of task-relevant target events (Donchin, 1981), or as an index of a transient postdecision closure of current cognitive processes, presumptively evoked through a frontal pacemaker exerting widespread control on subcortical and cortical systems (Desmedt and Debecker, 1979; Desmedt, 1981a,b). Desmedt suggested that the P300 may represent a kind of interrupt function between distinct serial cognitive processes, possibly in conjunction with target updating in short-term memory (Desmedt et al., 1984). Earlier components such as the N100 or N200 were contrarily related to predecision processes in conjunction with target selection (Hillyard et al., 1973; Desmedt and Robertson, 1977; Ritter et al., 1979; Hillyard and Picton, 1979; Naatanen and Michie, 1979; Hansen and Hillyard, 1980; Harter and Guido, 1980; Desmedt, 1981a; Knight et al., 1981; Ritter et al., 1984). During comparisons of the tactile and the auditory domain, the electrical sign of ERP components associated with target selection were found to be reversed. Furthermore, these “processing positivities”, such as the P100 (instead of the N100 seen for auditory targets), and even earlier positivities, such as the P40 (Desmedt et al., 1984), were more dominantly represented in the ERPs found in the tactile domain as compared to the auditory domain (Desmedt and Robertson, 1977).

After peripheral somatosensory stimulation, the contralateral response from the parietal cortex represents classical early somatosensory components, N20, P27, and P45 that are preceded by the P14 far-field (Fig. 2). The P14 reflects the volume-conducted volley ascending in the medial lemniscus, while the N20 represents the earliest cortical response from Brodmann area 3b in the SI. Comparing target to non-target stimuli, revealed that both the lemniscal far-field P14 and the contralateral cortical N20 consistently superimpose on each other (Fig. 2), suggesting that up to its arrival in area 3b the ERP is not dramatically influenced by a given task (Desmedt and Robertson, 1977; Desmedt et al., 1984). Afterwards, the response to target and non-target stimuli positively diverges at a mean latency of 25 ms, occurring in the parietal cortex and initiating the P40 (Desmedt et al., 1984). The occurrence of this P40 ERP component suggests that the “set,” or bias associated with the subject's preparation for target selection in serial tactile tasks, is indexed by an early change in the cortical electrical response (Fig. 2).

The question of when cognitive processing is initiated has been intensively debated (Hillyard and Picton, 1979). Before the description of the P40 (Desmedt et al., 1984), ERP components due to tactile stimuli were shown to diverge between 50 and 80 ms after stimulus presentation (Desmedt and Robertson, 1977). This

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