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Tactile remapping: from coordinate transformation to integration in sensorimotor processing

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Tactile localization entails the transformation of the initial skin-based location into an external reference frame that accounts for body posture and subsequent flexible integration of these two reference frames. The mechanisms underlying this tactile remapping are not well understood. Notably, there is a gap between the principles uncovered by psychophysical research and the mechanistic explanations offered by neuroscientific studies. We suggest that spatial localization is best viewed as a process of integrating multiple concurrently active spatial representations rather than a sequential transformation process. To achieve integration, large-scale interactions are required that link these different representations. Coordinated oscillatory activity may be a suitable mechanism that allows parallel representation of multiple spatial formats and the formation of an integrated location estimate.

Reference frames for spatial processing

To act toward an object in the world, the brain must determine the object's location, relative to the body, from the pattern of activity elicited by the sensory receptors. In touch, spatial location is initially defined by which receptors on the skin are active; that is, in a skin-based or anatomical reference frame. However, because our limbs move in space as well as relative to each other, the brain must integrate the skin location with current body posture to localize touch in space [1], a process referred to as tactile remapping [2]. The reference frame of the resulting spatial coordinate is often denoted as external [2], indicating that it is independent of body posture (see Glossary). To illustrate this with an example, picture yourself sitting on the lawn in a park for a picnic and imagine you are feeling a tickle on your hand. Where you have to direct your gaze to detect the cause of the sensation and how you have to move the other hand to swipe away the insect causing the tickle differ greatly depending on whether you are leaning on the hand behind your back or holding a plate in front of you with that hand. Whereas the skin-based location of the stimulus is identical in the two cases, its external location is different, which determines the movements necessary to act on the stimulus.

Other sensory systems code spatial information in their own modality-specific reference frames that are determined by the structure of their sensory surface. For example, in the visual system an object's location is defined by its location on the retina, which is activated by the light reflected by the object, referred to as an eye-centered or gaze-centered reference frame [3]. Object location can, furthermore, be referenced to a body part or an effector; that is, the body part executing an action resulting, for example, in a head-centered or hand-centered reference frame. Finally, to guide action, spatial information for motor commands appropriate to attain a target object must be deduced from sensory, spatial information [4].

The conversion of spatial information from one type of reference frame into another, as in tactile remapping, is referred to as a coordinate transformation. A dominant view of coordinate transformations has been that the brain converts different types of spatial information into one common reference frame [5–8]. This strategy would appear useful because it allows comparing and integrating information from all senses and for all effectors. A research focus arising from this view has been to determine which of many possible reference frames (e.g., gaze-centered, head-centered, body-part-centered) may be the relevant one for a given process or brain region under scrutiny (Figure 1A). However, recent behavioral, electrophysiological, and neurophysiological evidence suggests that information is usually available in multiple reference frames, all of which may influence behavior, presumably according to a weighting scheme [9–13] (Figure 1B,C). This alternative view implies that information is integrated across multiple spatial reference frames and suggests that the task context may affect spatial processing via top-down signals [14,15].

This new view shifts the emphasis with respect to the potential mechanisms that mediate coordinate transformations and reference frame integration, now raising the questions of how information is selectively routed and integrated and how fine-tuned weighting of information

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Glossary

Allocentric reference frame: a reference frame that is independent of the subject, its origin and axes relating to some entity in the environment. For example, a geographical coordinate system might have its origin at the North Pole and its coordinates are independent of the location, orientation, and posture of a subject.
Alpha-band activity: oscillatory electrical brain activity in the frequency range of about 8–12 Hz.
Anatomical reference frame: in tactile localization, a reference frame anchored to the skin, also referred to as a skin-based reference frame.
Beta-band activity: oscillatory electrical brain activity in the frequency range of about 13–30 Hz.
Coordinate system: a system that uniquely defines the spatial location of an event or object.
Coordinate transformation: obtaining an object's location in one coordinate system from its location as specified in another coordinate system; for example, the calculation of a tactile object's gaze-centered location based on its location on the skin, posture, and gaze position.
Cue validity: the probability that some contextual information correctly predicts an event in space, time, or meaning; for example, a cue indicating on which side a task-relevant target stimulus will occur. Effects of cue validity on stimulus processing are usually interpreted to indicate attentional orienting and, thus, susceptibility to top-down modulation.
Egocentric reference frame: a spatial reference frame whose origin and axes depend on the location, orientation, and/or posture of the subject. Skin-based, eye-centered, and gaze-centered reference frames are all instances of egocentric reference frames.
Event-related potential: an electrophysiological brain signal originating from the coordinated activity of large neuronal pools, measured with electroencephalography, that is time locked to a specific sensory, cognitive, or motor event.
External reference frame: in tactile localization, the reference frame used to refer to tactile location after body posture has been integrated with skin location. 'External' serves as a placeholder that leaves open which of several possible reference frames may be used by the brain for this purpose (e.g., eye, gaze, head, or hand-centered).
Gamma-band activity: oscillatory electrical brain activity in the frequency range of about 30–100 Hz.
Latent variable: a variable that is assumed by a theory or model but cannot be observed directly.
Reference frame: in the context of spatial information, a coordinate system and its anchor, in relation to which spatial information is measured and represented.
Rhythmic entrainment: the modulation of the timing of the action potentials of individual neurons to occur in synchrony with the action potentials of other neurons, resulting in rhythmically coordinated firing across large neuronal pools. This mechanism may serve to recruit individual neurons for the processing of specific functions or stimuli.
Saccade: a rapid, directed eye movement between two visual fixations.
Sensorimotor contingency: the systematic co-occurrence of sensory and motor events. For example, when the hand reaches the nose to scratch an itch, tactile, proprioceptive, and visual stimulation will regularly be similar for separate repetitions of the movement; accordingly, the location of the itch may be reached by attempting to reinstate this specific set of multisensory stimulations.
Spike-field coherence: the degree to which an individual neuron's action potentials are rhythmically entrained with a local field potential, an extracellularly recorded potential that reflects the average activity of a local neuronal population.
Tactile remapping: the transformation of a coordinate in a skin-based reference frame into a coordinate in an external reference frame by integration of posture information.

can be achieved. Here we suggest that information transfer through large-scale connectivity, implemented as coordinated rhythmic neuronal activity, may be an important factor that enables the flexible use of reference frames. Thus, the parallel representation of space in multiple reference frames may be implemented by a distributed neural code that allows a flexible location estimate by integrating original and transformed sensory representations, modulated by contextual factors like cue validity and long-term learning of sensorimotor contingencies.

The research conducted in psychophysics, neurophysiology, and electrophysiology has often focused on different aspects of coordinate transformations and reference frames and, therefore, a convergent picture of these processes is currently difficult to draw. We focus here on touch to explore how findings from the various neuroscientific methods may eventually converge to a common understanding.

Tactile localization: transformation and integration

A common approach to investigating the functional principles and neural implementation of sensorimotor spatial processing is to assess the behavioral and neural consequences of experimentally misaligning different reference frames. In the tactile modality, skin-based and external reference frames can be brought into conflict by systematically manipulating limb posture, most commonly by limb crossing; for instance, a right hand (skin-based reference frame) crossed over the body midline is then located in left space (external reference frame). Effects of such a conflict have been investigated in sensory discrimination tasks. For example, a tactile cue located near a visual target stimulus has been shown to accelerate visual discrimination (Figure 2A). For short cue–target intervals – that is, when the tactile cue occurred up to 60 ms before the visual target – visual discrimination was enhanced on the side of space belonging to the anatomical side of the hand that received the tactile cue. The right hand accelerated right-side visual target discrimination even when the hands were crossed, with the right hand located in left space, indicating the use of a skin-based reference frame. By contrast, for long cue–target intervals (>180 ms), the tactile cue facilitated visual discrimination at the external location of the touch (e.g., left space for tactile stimulus at the crossed right hand), indicating the use of an external reference frame [16] (Figure 2A). Similarly, saccades to tactile stimuli on crossed hands have been observed to be directed initially toward the hand's anatomical side [17,18] when the saccade was elicited with a short latency. Such saccades were corrected around the time at which correctly directed saccades were usually elicited [19], suggesting that the external touch location becomes available later than the skin-based one.

These experiments suggest that tactile location is first represented in anatomical, skin-based space, then remapped by taking into account posture, and subsequently represented in external space (Figure 1A). However, recording of event-related potentials during tactile remapping experiments shows that components in the time range of 100–140 ms after tactile stimulation can reflect both anatomical and external spatial coding, suggesting that both reference frames are concurrently active [10] (Figures 1B and 2B). In this view, the reliance on external spatial coordinates in the abovementioned cueing experiment reflects strategic dominance of the external reference frame rather than a mandatory reference frame switch due to transformation.

This interpretation is supported by the finding of marked performance impairments in many other tactile tasks with crossed hands; for example, in temporal order judgments (TOJs) about which of two tactile stimuli, one on each hand, occurred first. Like the effects on stimulus detection discussed above, the effects of hand posture on TOJs are thought to originate from a conflict between skin-based and