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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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Keywords: tactile localization; reference frame; tactile remapping; top-down control; oscillatory activity; parietal cortex.

1364-6613/

http://dx.doi.org/10.1016/j.tics.2015.03.001

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

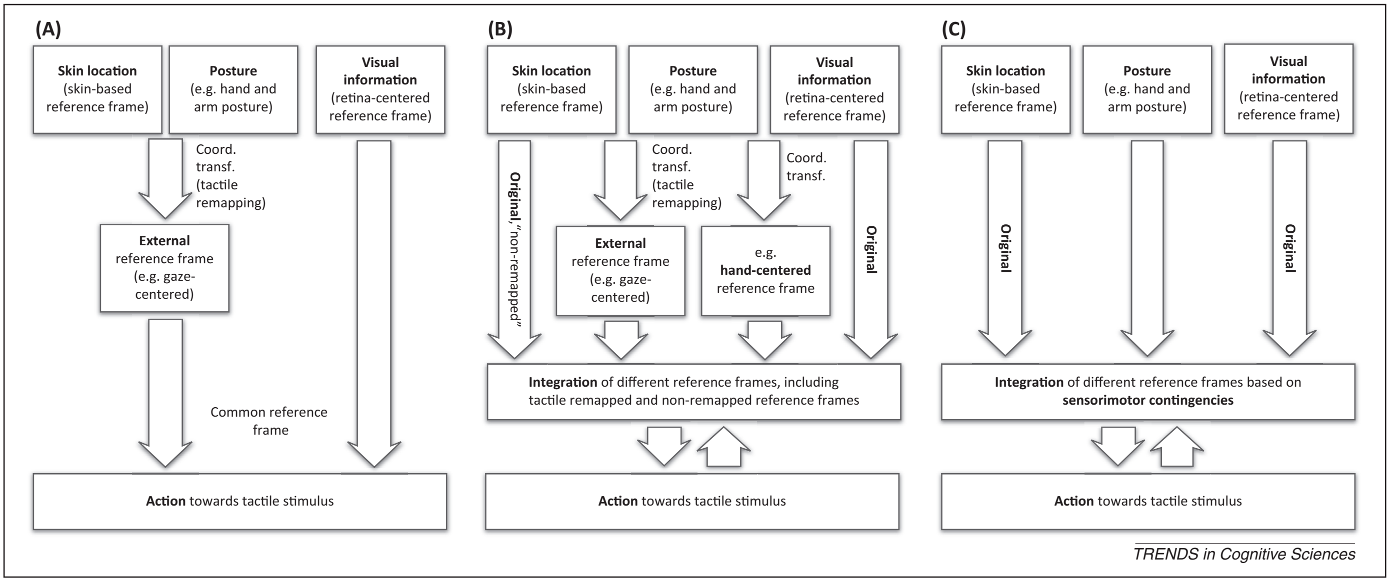

Figure 1. Coordinate transformations and tactile remapping. **(A)** Remapping view: Skin-based information is integrated with posture into a gaze-centered reference frame, allowing direct integration with other sensory information for action control. Effects observed in behavior are attributed to remapping. **(B)** Integration view: Information is transformed, for example by integration with posture. Skin-based tactile information is integrated with remapped information to derive a spatial estimate to guide action, which itself may modulate the spatial estimate. Behavioral effects are attributed to the integration process. **(C)** Sensorimotor contingency view: Statistical correspondences of information in different reference frames are learned and stored as probability distributions. Consequently, coordinate transformations occur implicitly rather than through explicit computation. Behavioral effects are attributed to the statistical properties of the learned sensorimotor correlations.

external reference frames with crossed hands [5,12,14,20,21]. As demonstrated by such studies, this conflict occurs even when the task requirements are non-spatial (here, temporal), allowing the investigation of automatic, task-independent spatial processing [2].

Crossing effects were originally suggested to result from an impairment of coordinate transformation [5,22] induced by the unusual hand crossing (Figure 1A). In line with this idea, event-related potentials following tactile hand stimulation are modulated by hand crossing even during passive stimulation [23–25], possibly indexing a modulation of automatically triggered spatial transformations during tactile processing.

However, other findings suggest that crossing effects may reflect the integration of spatial information in different reference frames after tactile remapping has been

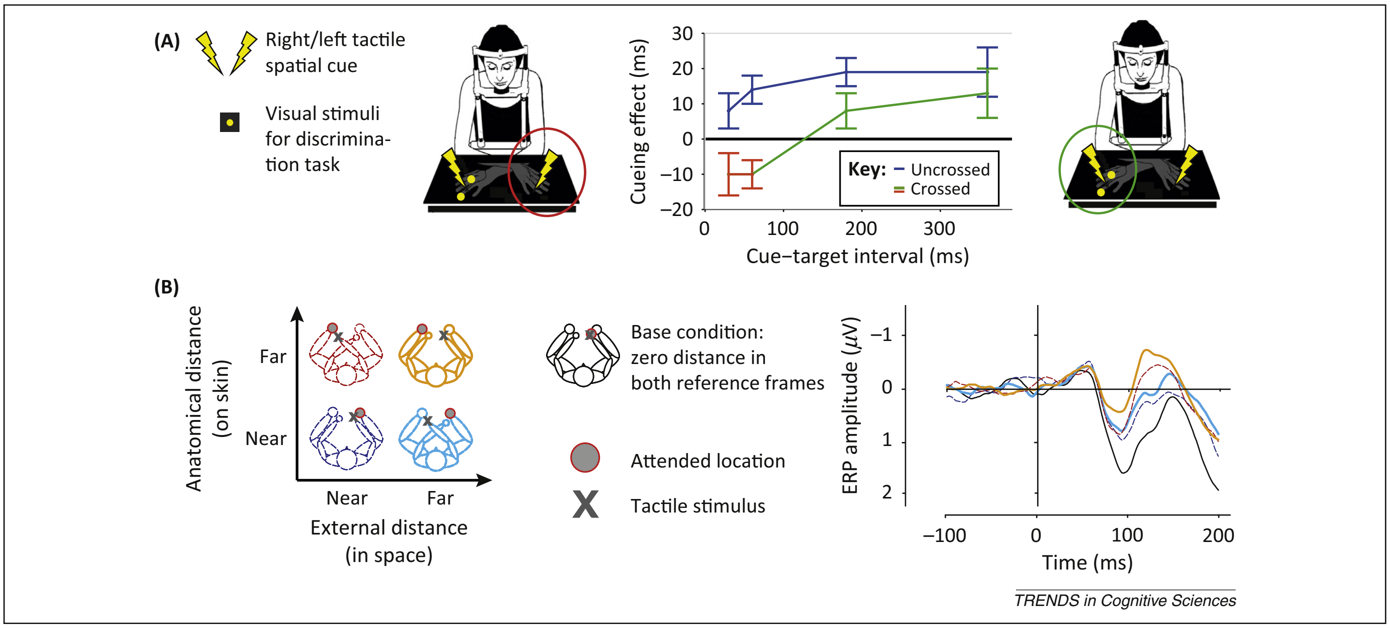

Figure 2. Consecutive and concurrent activation of skin-based and external reference frames. **(A)** Effects of hand posture on tactile cueing of visual decisions. Tactile cues on uncrossed hands accelerate visual detection near the hand (middle, blue). With crossed hands, the effect of the tactile cue depends on the cue–target interval. For short intervals (middle, red), visual decisions are accelerated on the stimulated hand's body side. Longer intervals (middle, green) lead to acceleration on the hand's side of space, suggesting consecutive activation of skin-based and external reference frames. **(B)** Recording of event-related potentials (ERPs) to tactile stimuli on the right hand while attention is directed to one of the feet (left). Parietal ERPs (right) are modulated by skin-based and external reference frames. The ERP amplitude modulation between 100 and 140 ms increased with distance in both reference frames compared with stimulation at the attended location. This implies that the two reference frames were concurrently active. (A) adapted, with permission, from [16]; (B) adapted, with permission, from [10].

completed (Figure 1B). In this view, several coordinate transformations might occur in parallel and, after remapping skin-based location with posture information, the resulting external location estimate would then be integrated with the original, skin-based location and, potentially, further information that may be available in different spatial formats. In this model, crossing effects reflect a conflict in the integration of disparate spatial information rather than difficulty in coordinate transformation.

Several experimental findings corroborate the view that the behavioral effects observable in the context of tactile remapping predominantly index spatial integration (Figure 1B). First, saccade performance to visual–tactile stimuli reflected stronger multisensory spatial integration effects for crossed than uncrossed hands [18] and this result was best explained by positing interactions of the original, skin-based location signal with the transformed tactile signal and the visual signal in a presumed multisensory map according to spatial interaction principles known from multisensory physiology [26]. Second, tactile localization has been shown to be subject to top-down modulation, as evident in modulations of the use of reference frames by task context [14,27,28]. When a short-term memory task had to be performed concurrently with a tactile TOJ task [14], increased difficulty of the memory task ameliorated crossed-hands performance in the TOJ task; that is, increased memory load reduced the hand-crossing effect. It seems implausible that an additional task would improve coordinate transformation in the TOJ task. Third, when the limbs are crossed twice – for example, by crossing the arms and additionally crossing the fingers of the two hands back into their regular spatial hemifield – the crossing effect for touch on the fingers is strongly reduced [21,29]. If crossing *per se* were responsible for the deterioration of tactile localization, double crossing should have detrimental consequences for behavior. By contrast, the amelioration of localization performance by double crossing is well in line with the integration account, given that the fingers are located in their regular hemifields.

Taken together, these results suggest that the modulation of the crossing effect results from a change of the integration process; for example, of the weights assigned to the different reference frames. Whereas these findings imply that many behavioral effects observed in the context of tactile localization reflect integration of information available in multiple spatial formats, they do not dispute that coordinate transformations are executed by the brain (Figure 1B). However, some theoretical approaches would take this step and suggest that coordinate transformations are an implicit, emergent property of spatial integration (Box 1 and Figure 1C).

In summary, like other multisensory processes [30–33] tactile localization appears to involve the derivation of an optimal sensory estimate by integrating all available cues, even when the different signals provide strongly conflicting information [2,34,35]. The integrated location estimate can then serve to plan and execute actions in response to the tactile event; for example, a location judgment [2,36], a saccade [19], or a hand reach [37,38] (Figure 1B). Flexibility in the use of reference frames has also been observed in other modalities. fMRI responses to visual stimuli moving in the periphery reflected gaze-centered coding during a task demanding foveal attention but head-centered coding when attention could be directed freely [39]. Furthermore, posterior parietal and premotor regions appear to encode visual targets for hand reaches primarily in gaze-centered coordinates but proprioceptive targets in head-centered coordinates [9].

Box 1. Explaining coordinate transformation through sensorimotor contingencies

Action-oriented views posit that cognition is defined by the sensorimotor contingencies that an organism acquires while acting on the world during ontogenetic development [78–81]. In this view, multisensory integration is learned by extracting the pattern of co-occurrences of the signals from the various modalities and the changes in such signals resulting from the organism's own actions. Crucially, in such a framework coordinate transformation can be viewed as an emergent byproduct of extracting contingencies (see Figure 1C in main text) rather than a dedicated cognitive function.

Information of the different senses related to a common spatial location will naturally co-occur, for example, during the processing of visual and proprioceptive information related to a specific hand location. The external location of touch would emerge as the repeatedly experienced correlation of the locally specific activity of skin receptors with proprioceptive and visual information about limb position. In goal-directed action, motor-related signals are associated with sensory co-occurrences. Accordingly, actions and their spatial parameters can be defined by specifying (part of) the sensory consequences that the organism intends to realize [81,82], an idea that was formalized in ideomotor theory by William James in the 19th century [83]. To illustrate, picture scratching an itch on the nose. Relief of a nose itch has repeatedly co-occurred with specific hand movement commands and the related proprioceptive signals and with vision of the hand near the face. Thus, to cure a nose itch, the organism can attempt to reinstate these sensory experiences.

In line with this framework, recent computational work has shown that coordinate transformations emerge in a network that is trained with different types of sensory information (e.g., joint angle, visual location, eye position) and learns to extract the density (that is, mean and reliability) of the latent variables underlying these co-occurring signals (here, hand location in space) [55]. Thus, the network is able to integrate information although spatial transformations are not explicitly implemented but emerge from the learned correlations between sensory and motor-related signals (see Figure 1C in main text). Furthermore, it was shown that the receptive field characteristics of units of such a network can resemble those found in neurophysiology [55].

This type of approach thus suggests that the distinction between multisensory integration and coordinate transformation may be artificial and stresses the role of sensory integration, well in line with the recent developments highlighting integration over transformation that we have described for the field of tactile spatial processing.

Neuronal implementation of reference frames

Many neurophysiological studies of spatial reference frames have focused on saccades and reaches to visual rather than tactile targets. Although initial studies investigating receptive fields and tuning curves of single neurons suggested that different types of spatial information like eye, hand, and target position can be represented in one common reference frame [6–8], other studies showed that many frontal, temporal, and parietal neurons exhibit 'intermediate' reference frames [40–46]. For example, a neuron might shift its visual tuning curve by 10° when the eye moves 20°, indicating a reference frame intermediate between eye- and head-centered coordinates.

Furthermore, neurons often exhibit so-called gain fields; that is, their firing rate undergoes systematic modulation in dependence of effector position (e.g., of the eye) [40–43,47,48], allowing parallel coding of several reference frames within a neuronal population.

For touch, research has concentrated on the ventral intraparietal area (VIP) in the posterior parietal cortex and on the ventral premotor cortex (PMv). In macaques, VIP neurons respond to touch, vision, audition, and vestibular information, although tactile information has the shortest response latencies, suggesting that this region's main role may be in the tactile domain [40]. Vestibular information was found to be coded in head, body, and intermediate reference frames [42]. Touch to the head is presumably coded in a head- or body-centered reference frame [40], whereas vision and audition in near space are coded in eye, head, and intermediate reference frames [40,41]. Others have reported that visual and auditory space appear to be linked to tactile receptive fields in VIP and PMv, so that, for example, a neuron with a tactile receptive field on the hand always responds to the visual space near that hand [49–52].

The omnipresence of intermediate reference frames and gain fields might suggest either that coordinate transformations are performed in many brain regions or that spatial information is represented in parallel in multiple reference frames throughout the brain, neither view being compatible with a purely serial transformation concept. Furthermore, it remains open how these neuronal findings may relate to behavioral data. Attempting to bridge this gap, computational approaches have replicated neuronal patterns in intermediate layers of recurrent networks that provide different mathematical implementations of spatial coding and coordinate transformation; for example, using basis functions [53], probabilistic population coding [54], or density estimation [55]. Importantly, networks that implement probabilistic principles can account for both coordinate transformation and sensory integration and thus provide a framework for the natural integration of these two seemingly separate functions [13,54–56] (Box 1).

In humans, transcranial magnetic stimulation (TMS) of the putative homologs [57,58] of VIP and PMv appears to impair spatial matching between the senses, presumably by disrupting the integration of proprioceptive posture information with skin location [59–62]. For example, whereas a tactile stimulus to a crossed hand normally facilitated detection of a visual stimulus at the matching location in external space, it facilitated detection of visual stimuli on the hand's body side (that is, in the space opposite to where the crossed hand was located) after TMS over putative VIP [59]. Note that although these findings, like the behavioral results, are often interpreted as indicating reference frame transformations from skin-based into external coordinates, they are equally compatible with the notion of external coordinates (e.g., from vision) being transformed into tactile space [63]. Furthermore, whereas usually such results have been interpreted to indicate that TMS disrupts coordinate transformation, they can be just as well be viewed as indicating a disruption of information integration and weighting.

Dynamic coordination for integration of reference frames

With the shift of focus in spatial processing from local transformation mechanisms to the integration of multiple information sources, the study of single-neuron responses and the modeling of neuronal networks leave open several essential questions. One key question is how information flow is coordinated between the regions involved in the transformation and integration of multiple coordinates to allow flexibility for top-down modulation and weight adjustments. Furthermore, whereas we now know that information is integrated, it remains open how the multiple reference frames evident in single neurons can be kept separate at the population level and be selectively communicated to other regions. We suggest that answers to these questions may require investigation of the large-scale mechanisms that link functional and neuronal levels and are implemented by oscillatory brain activity; that is, the rhythmic coordination of neuronal firing.

Several aspects of oscillatory brain activity seem to be optimally suited for implementing the processes discussed here. First, oscillatory activity has been proposed as a prime mechanism to account for both intra- and interregional neuronal coordination (Box 2), a process we have identified above as crucial for spatial integration. Second, oscillatory activity has been related both to top-down and bottom-up processing. It is thought to instantiate functional coupling across regions on multiple timescales, allowing flexible coordination of local and distributed neuronal pools

Box 2. Possible roles of oscillatory networks in merging spatial reference frames

Functional coupling [66] between different brain regions can be established by cross-frequency coupling [69,84], phase correlation [85,86], and power envelope correlations [87]. These coupling processes could mediate flexible weighting of spatial information in multisensory regions like the posterior parietal cortex. For example, communication between parietal and visual areas may intensify by means of oscillatory coupling through top-down modulation when visual information is relevant for a tactile task, thereby increasing the probability that parietal neurons are recruited into the network that represent the gaze-centered reference frame.

Consistent with this view, cognitive factors like cue validity can influence tactile processing via anticipatory oscillatory activity [73,75]. Moreover, the specific regions constituting a network are determined by task context. For example, different parietal regions expressed stimulus-related oscillatory activity when participants had to saccade, compared with when they had to reach, to tactile targets [11,74]. Accordingly, regionally specific connectivity may, in turn, affect spatial processing and the weighting of different spatial cues via feedback loops in a top-down fashion. Bottom-up modulation of tactile processing might also emerge through regional connectivity; for example, strong, spatially specific oscillations in retinotopic visual areas could modulate tactile processing in the parietal cortex through rhythmic entrainment potentially promoting gaze-centered coding for touch.

In summary, oscillatory brain networks flexibly emerge during cognitive processes and rapidly adapt to the current context and might therefore be critical for the integration of spatial information across currently active network nodes. However, in addition to noninvasive studies using electroencephalography and magnetoencephalography, intracortical recordings using, for example, spike-field coherence [71] could improve our understanding of transformation and integration processes.

[64–67]. Consequently, a single region might participate in different functional networks or carry different types of information that are organized in different spectral communication channels [67,68]. In the context of spatial integration, different reference frames could be made available in parallel through this mechanism. Finally, oscillatory activity provides a dimension to neuronal coding that is not based on a rate code. For example, in some mouse hippocampal neurons phase precession, but not firing rate, was found to dynamically encode the animal's distance from a location [69,70]. In the context of spatial coding, the observation of partially shifting receptive fields [40–46] might originate from pooling across all action potentials of a single neuron, ignoring their phase relationship with the population. A different interpretation may result when selectively focusing on a specific frequency range or considering neuronal spiking relative to the phase of an underlying network oscillation [71,72] (Box 2).

Although these suggestions are currently speculative, first evidence has linked oscillatory activity with various aspects of tactile remapping and spatial representation. Activity related to tactile saccade [11,73] and reach targets [74] at uncrossed and crossed hands has been observed at different oscillatory frequencies in partially overlapping posterior parietal regions (Figure 3). Alpha- and gamma-band activity reflected gaze-centered tactile stimulus coding in posterior regions whereas gamma-band activity concurrently reflected skin-based coding in central regions. By contrast, beta-band activity reflected skin-based, anatomical stimulus coding across rolandic and parietal regions [11]. Thus, specific frequency bands may be associated with specific spatial processes and, accordingly, transmit specific reference frames. Furthermore, consistent with the behavioral findings suggesting top-down modulation of reference frame integration, both alpha- and beta-band activity in anticipation of tactile stimulation can be modulated by the spatial validity of the cue indicating the location of tactile stimulation [75].

Consistent with the association of posterior alpha-band activity with external tactile coordinates, lateralized TMS at alpha frequency applied over the medial posterior parietal cortex can spatially bias visual [76] and tactile [77] processing toward one hemifield. In touch, this bias occurs in external coordinates such that which hand is affected by TMS changes when the hands are crossed [77]. Whether alpha-band activity also plays a specific role in VIP, and whether it would be associated with external coordinates there as well, remains an open question.

These findings do not suggest that spatial representation and integration are the sole purpose of oscillatory activity. Rather, oscillatory brain activity provides mechanisms that are suited to implement the specific requirements of spatial integration, as has been suggested for other functional domains. Accordingly, they may be instrumental for investigating the questions that emerge from the spatial integration view we have put forward.

Concluding remarks

Significant progress has been made in specifying how humans process spatial information for touch, emphasizing a crucial role for the integration of spatial information coded in multiple reference frames that are represented in parallel. Recent work exploring large-scale oscillatory activity in the brain may point to possible neural implementations of such functional integration. The principles of parallel coding and large-scale communication mediated by oscillatory brain activity may allow us to develop a

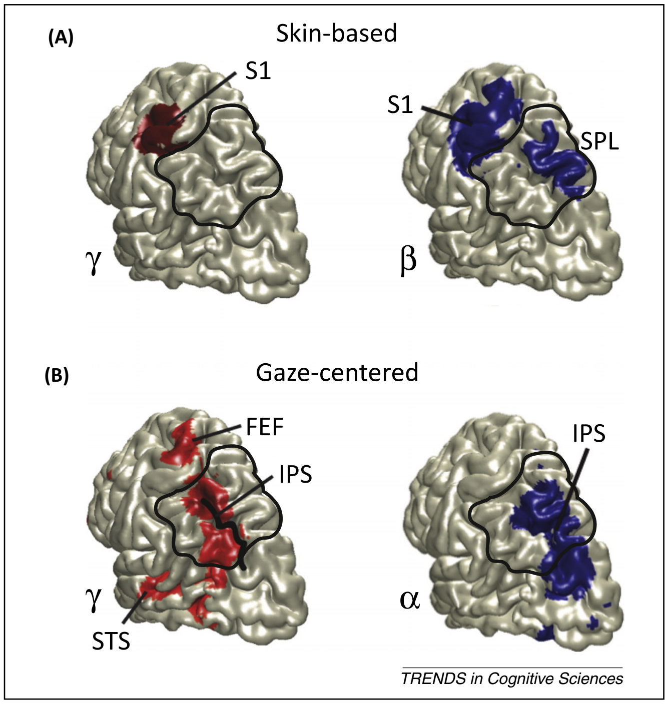

Figure 3. Oscillatory signatures of tactile remapping. Subjects had to saccade toward a finger of their hand cued by a tactile stimulus [11]. Dissociating the side of a tactile stimulus in skin-based **(A)** and gaze-centered **(B)** reference frames (e.g., left hand in right hemifield), allows the investigation of lateralized modulations of oscillatory activity during motor planning. Somatosensory cortex (S1) and the posterior parietal cortex (PPC) (black outline) were concurrently active during remapping in the gamma band (red). Lateralization of the oscillatory activity depended on skin-based (A) and gaze-based (B) target position, respectively (results pooled across hemispheres). Furthermore, alpha- and beta-band activity (blue) reflect different reference frames within the PPC. The integrative role of beta-band activity in the visual hierarchy [88] may generalize to the tactile domain, integrating information across S1 and the PPC in a skin-based reference frame. By contrast, alpha and gamma appear to reflect the remapped target position in the PPC. Abbreviations: IPS, intraparietal sulcus; FEF, frontal eye field; STS, superior temporal sulcus. Adapted, with permission, from [11].

Box 3. Outstanding questions

- Which factors, for example pertaining to task context, govern the weighting of different reference frames?
- What are the relationships between behaviorally assessed reference frame weight adjustments and modulations of oscillatory brain activity? For example, does stronger reliance on a given sensory reference frame result in stronger connectivity between the respective sensory regions and multisensory (e.g., parietal and premotor) regions?
- Can we identify general principles in the relationships between specific reference frames and oscillatory activity? For example, are specific frequency bands associated with the same type of reference frame across modalities as well as across cortical regions?
- Can findings about oscillatory brain mechanisms inspire models of coordinate transformation and sensory integration? For example, could the neuronal spike code support different reference frames depending on the phase of an underlying network rhythm, thus offering a mechanism to segregate information?

comprehensive view that reconciles findings from various fields including single-cell neurophysiology and computational studies and accounts for top-down influences on spatial representations. At present, many aspects of this view remain speculative and raise questions for future research (Box 3) that may elucidate how tactile space is processed and modulated by other cognitive processes.

Acknowledgments

The authors thank Stephanie Badde for helpful discussion. They are grateful for support by the Deutsche Forschungsgemeinschaft (DFG) (SFB 936/A2/A3/B1/B2 to A.K.E., T.H., and B.R.; Emmy Noether Programme HE 6368/1-1 to T.H.) and the EU (ERC-2009-AdG-249425 to B.R.; ERC-2010-AdG-269716 to A.K.E.; FP7-ICT-270212 to A.K.E.).

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