



Review

Multisensory contributions to the perception of vibrotactile events

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ABSTRACT

We argue that audio-tactile interactions during vibrotactile processing provide a promising, albeit largely neglected, benchmark for the systematic study multisensory integration. This article reviews and discusses current evidence for multisensory contributions to the perception of vibratory events, and proposes a framework to address a number of relevant questions. First, we highlight some of the features that characterize the senses of hearing and touch in terms of vibratory information processing, and which allow for potential cross-modal interactions at multiple levels along the functional architecture of the sensory systems. Second, we briefly review empirical evidence for interactions between hearing and touch in the domain of vibrotactile perception and related stimulus properties, covering behavioural, electrophysiological and neuroimaging studies in humans and animals. Third, we discuss the vibrotactile discrimination task, which has been successfully applied in the study of perception and decision processes in psychophysical and physiological research. We argue that this approach, complemented with computational modeling using biophysically realistic neural networks, may be a convenient framework to address auditory contributions to vibrotactile processing in the somatosensory system. Finally, we comment on a series of particular issues which are relevant in multisensory research and potentially addressable within the proposed framework.

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1. Introduction

The feeling of skin dryness or moistness that arises when we rub our hands against each other is subjectively referred to the friction forces at the epidermis. Yet, it has been demonstrated that acoustic information also participates in this bodily sensation, because altering the sound arising from the hand rubbing action changes our sensation dryness/moistness at the skin. Above and beyond the mere curiosity of this phenomenon, dubbed the *parchment-skin illusion* [53], this illustration touches on the very fundamental issue of how the interplay between different sensory systems contributes to our perception of the world and of ourselves. There is growing consensus around the idea that a satisfactory account of multisensory processes will be integral to any comprehensive theory of perception [13,22,80]. Indeed, there are multiple examples of how interactions between the senses can have a dramatic impact on sensory and perceptual processes, both measured behaviourally as well as in terms of physiological correlates of neural activity [11,101,107]. Although the amount of research effort devoted to understand multisensory interactions has been remarkable over the last decade, the stress has been primarily placed on a few particular modality pairings (i.e., audio-visual being the most prominent one, possibly followed by visuo-tactile) and perceptual domains (i.e., spatial perception, speech perception, object recognition, and more recently, temporal perception). Here we focus on the specific case of auditory–tactile interactions in the perception of vibrotactile events. We think that this case is of particular interest in its own right because of the close relationship that exists between the senses of hearing and touch. In fact, it is surprising that despite the relatively good knowledge that currently exists regarding the physiology and psychophysics of vibrotactile processing at a unisensory level and the close relationship between the senses of hearing and touch (see next section), the multisensory aspects of vibrotactile perception have received little attention in the literature.

In our view, understanding the neuronal and cortical mechanisms underlying multisensory perception does not only require empirical observations of behavioural or neural responses, but also theoretical and computational analyses of the processes putatively involved. Computational models explicitly link neurophysiological and behavioural experimental observations by the construction and simulation of microscopic models based on local networks with large numbers of neurons and synapses that lead to the desired global behaviour of the whole system. Biophysically realistic microscopic models are expressed by a dynamical system due to the fact that processing does not operate in a completely feed-forward fashion, since recurrent feedback is also present and there are good grounds for supposing that these feedback connections have a functional role in most aspects of brain processing [28]. To understand information processing, we need to understand the dynamic contributions from feed-forward and feed-back processes over time, and this involves more than a one-sweep feed-forward computation [43,67,86]. Many recent examples in the neuroscience literature (e.g., working memory, attention, decision-making) advocate for a dynamical system approach [8,18,86,113] that allows us to discover the neuronal computation underlying specific brain function by solving the neurodynamical inverse problem of finding the connectivity structure from which the measured neuronal correlates emerges.

In the present article, we will briefly review some relevant aspects about the perception of vibrotactile patterns in the senses of hearing and touch, with a special stress on studies addressing audio-tactile interactions. Then we focus on one particular methodological approach based on vibrotactile discrimination task which we have recently applied to address somatosensory perception using a combination of psychophysical and computational analysis

tools. We argue that this type of methodological approach can be adopted to help address several important aspects of audio-tactile interactions and multisensory perception in general. Finally, we will point out several research questions which we think are relevant, and potentially addressable within the proposed context.

2. Some similarities and differences between hearing and feeling

The case of auditory–tactile interactions in the processing of vibratory stimulation is one of the few types of multisensory interaction in which the two sensory modalities involved are sensitive to the very same kind of physical property (mechanical pressure in the form of oscillations). The tight correlation between the information content (oscillatory patterns) being conveyed in the two senses can potentially support interactions of an *integrative* nature at a variety of levels along the sensory pathways, from the most peripheral stages up to the cortical association areas of the central nervous system. Multisensory interactions of an *integrative* kind involve exploiting two correlated sources of information about the same external event, and go beyond mere *cue combination* between concurrent but qualitatively distinct cues that have a complementary nature. In the case of cue combination, each sensory modality provides information about a different aspect or property of an object, and their combination allows to maximize information (for example, we often inspect the front of an object visually whilst feeling its back shape haptically [75]). In the case of cue integration, each modality receives information about the same property of the external object, and the binding mechanism leads to an increase of the reliability of the sensory estimate about that property, via a reduction in the variance of the resulting percept (see [24]).

In the particular case of vibratory patterns, the senses of hearing and touch are not only sensitive to the very same class of physical events but, within a certain range of frequencies, the very same vibratory stimulus can be experienced simultaneously by the peripheral receptor organs of both sensory modalities (the basilar membrane in the cochlea and the skin). This is so despite the fact that the subjective sensation, or quality, that these stimuli produce on arrival to the central nervous system is of a radically different nature depending of the afferent pathway in which they have been transmitted (a sound vs. touch, respectively, though [10,98] discuss cases of confusions in certain conditions).

Von Békésy [112] already pointed out some similarities between the senses of hearing and touch, and went as far as to propose that the sense of touch could be used as a model for the study of some aspects of hearing (see also [37]). Amongst these similarities, he highlighted the analogies between the encoding mechanism at the respective receptor surfaces (i.e., similar deformation patterns of the basilar membrane and the skin upon stimulation), which lead to a similar experience of loudness in both senses. In fact, von Békésy mentioned the idea that these similarities might root partly in the evolutionary origins of the basilar membrane, which seemingly evolved from an area of skin which became increasingly sensitive to vibrations (see [70], for evidence of a primitive specialised vibratory detection system in the skin of some fish, called the lateral line). Of course, there are also limitations to the analogy between hearing and touch, of which von Bekesy was fully aware. For example, the quicker transduction times and superior sensitivity (in terms of absolute threshold) of the ear with respect to the skin (which von Békésy attributed to a higher density of receptors in the auditory system) produce a shorter latency from stimulation to full sensation in hearing than in touch. There is also a different range of vibratory frequencies to which each modality is sensitive. The skin has the capability to register very slow oscillations because it is sensitive

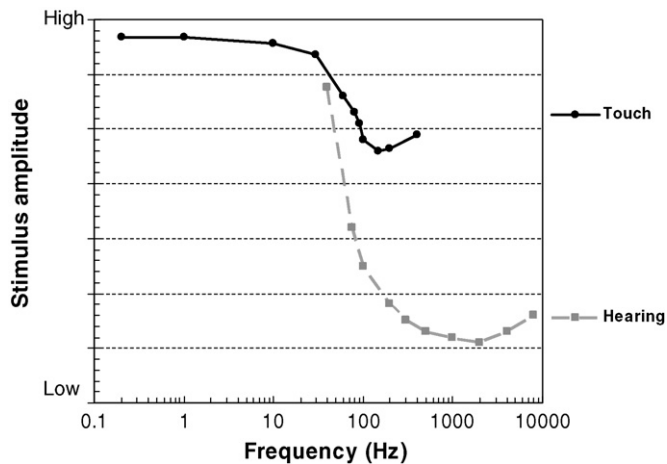


Fig. 1. Graph illustrating the relationship between the threshold amplitude necessary to elicit auditory and tactile vibratory sensations as a function of vibration frequency (figure adapted from [38]).

to mechanical pressure of non-vibratory nature (as low as 0.020 g at the fingertip, [114], although in order to produce a vibratory sensation², including that of flutter [52,111], the oscillations need to have a frequency above 3 Hz. In the auditory system the sensitive range goes from about 20 Hz to 20 kHz in young healthy adults (see [14]). Despite these important differences, one interesting aspect is that, albeit small, there is a window of overlap between the ranges of vibratory sensitivity of each modality that provides the basis for audio-tactile interactions of an integrative nature already at very early stages of information processing (see Fig. 1).

It must also be noted that the mechanical aspect of touch (i.e., not counting thermal or pain sensations) is transduced in the periphery by four essentially different types of mechanical receptors, each one having a particular morphology, sensitive range, receptive field size, and response pattern over time (see [52] for a review). Thus, the selective activation of different receptors yields distinct sensations (for example, that of steady pressure upon activation of Merkel and Ruffini endings, or that of tingling vibration upon activation of Meissner's and Pacinian corpuscles). All four types of receptors are commonly involved to different degrees in our haptic experience of contact with everyday objects and surfaces. The transduction of sound, on the other hand, does not involve such a rich variety of mechanoreceptors, with the inner and outer hair cells attached to the basilar membrane being at the base of acoustic transduction [71].

Finally, another distinction between the tactile and the auditory systems, especially relevant in the present context, relates to the functional organization of each sense in the central nervous system, and in particular in the sensory cortices. Whereas the cortical organization of the somatosensory system is strongly determined by a spatial-somatotopic arrangement [74,81], the auditory cortex seems to be primarily organized in regions containing neurons that are maximally sensitive to particular sound frequencies (i.e., tonotopic organization [69]; see also [82,87], for evidence in humans). Thus, in the sense of hearing, the frequency of a vibratory stimulus is in general reflected by the localization of the responsive neurons within the cortical surface encompassing the relevant subdivision of the auditory cortex. An interesting exception to this general (tonotopic) principle is found within the flutter range (5 Hz–50 Hz).

It is remarkable that, within this frequency range, the frequency content of vibratory patterns at the skin as well as at the ear seems to be reflected in the firing rate of the neurons of the respective sensory cortices (e.g., [91,92] for the somatosensory cortex; [2,63] for the auditory cortex).

3. Interactions between audition and touch

Given the similarities between hearing and touch in terms of the type of physical energy they are sensitive to, their functional properties and, their possibly related phylogenetic origins, one would expect to find a close interplay between these two senses during perception. In fact, the opportunity for cross-talk between hearing and touch is quite prevalent in everyday behaviours, given that most activities that produce tactile sensations also produce sound ([34,35,45]; for a discussion on the relationship of hearing and feeling in music perception). Yet, despite the pervasive association of tactile and acoustic experiences during everyday life behaviours, the sensory quality of these multisensory events is often dominated by one of the two modalities (for example, our experience of examining a textured surface is mostly tactile, whereas the experience of playing a musical instrument is chiefly auditory), and therefore the potential audio-tactile interactions goes mostly unnoticed for the observer in these naturalistic situations [64]. There are, however, several laboratory demonstrations of tactile influences on the perception of sound [9,73,93,103], of acoustic influence in the perception of touch [6,44,53,105,120–123], and of audio-tactile synergies in the detection of simple events [73,123].

From the literature addressing audio-tactile interactions it is worth to highlight the great deal of attention that has been paid in the recent years to the tactile influences on neural activity in the auditory cortex. This particular case has been investigated frequently in the context of the question of how early multisensory interactions take place during sensory processing (early being understood both in terms of latency and in terms of functional architecture). Several studies using a variety of physiological measurements of neural activity, including neuroimaging in humans [10,29,31,55,64] as well as single cell recordings in monkeys [7,33,57,95,96], show conclusively that tactile events can influence auditory evoked activity at the earliest stages of cortical processing. In particular, several animal electrophysiology studies demonstrate audio-tactile interactions in the secondary areas of the auditory cortex, including the caudomedial and caudolateral belt ([7,33,57,95]; see [54], for a review; see also [46] for evidence of anatomical connectivity). Non-invasive studies of neural activity in humans have also presented evidence for early tactile modulations of auditory activity based on the early latency of the interactive effects in electrophysiological [29] and magnetoencephalographical [10,64] recordings, or on their localization in fMRI studies [31,55,97]. All these results point very clearly to the presence of cross-modal influences in the auditory sensory cortex. It is perhaps less clear whether these early cross-modal influences can be interpreted as interactions of a specific nature (i.e., restricted by particular attributes of the stimuli such as common spatial location, congruent semantics, . . .) or else, they result from a global type of modulation whereby the presence of a tactile event modulates the excitability of whole regions of the auditory cortex (related to alerting, arousal, or overall weighting between modalities; see [21]). Supporting the latter type of explanation, Gescheider and Niblette [41] had already entertained the hypothesis that certain cases of auditory masking of tactile sensations in human psychophysics could be caused by a global inhibitory influence of the reticular formation on the sensory systems [49]. This idea was prompted by Gescheider and Niblette's [41] finding that audio-tactile masking

² Fast adapting fibres (FAI and FAII, terminated in Meissners and Pacini corpuscles, respectively) are the ones classically associated with the transduction of vibratory patterns at the skin.

effects were not modulated by the relative location of target and mask.

The behavioural consequences of these early audio-tactile interactions have been reported in the form of advantages in the detection of tactile events as a function of whether accompanying sounds were present or not [39,73,98,123]. For example, Schürmann et al. found a lowering of the threshold for detecting a 200 Hz sound when the acoustic stimulus was accompanied by the corresponding 200 Hz vibration at the skin of the hand (see [39], for a similar result using a 500 Hz vibration).

Audio-tactile interactions in the reverse direction, that is, the question of how acoustic input can influence processing in the somatosensory system have received much less attention, especially from a physiological point of view. For instance, Foxe et al. [29] reported early audio-tactile interactive effects in a human ERP study registered from post-central electrodes, placed over the somatosensory cortex. There are, however, several human behavioural studies documenting the existence of dramatic auditory influences in the perception of tactile events. For example, sound can influence the absolute threshold for tactile detection [37,39], the temporal resolution between tactile events [41], the spatial localization of tactile events [83], the perceived direction of tactile apparent motion [93,103,5,6], the perceived number of tactile events in a train of taps [5,6] and, specially relevant for the purposes of the present review, the perceived frequency content of a vibratory event at the skin [37,39,44,53].

In an early approach to address the hypothesis that auditory processing has an inhibitory effect on tactile processing, Gercheider et al. [37,39,44,53] used a masking procedure to evaluate the threshold for the detection of vibrotactile patterns at the fingertip as a function of sounds being presented concurrently. The results of those studies, however, were somewhat mixed as concurrently presented sounds sometimes lowered the detection thresholds for vibrotactile patterns of analogous frequency content [37,39,44,53], whereas in other occasions they produced a masking effect [37,39,44,53]. The authors noted the differential influence of sensory and response bias effects as the possible cause of the differences between studies (a point to which we shall return later).

More recently, Jousmaki and Hari [37,39,44,53] reported a curious phenomenon called the parchment-skin illusion, pointed out earlier in the introduction. This illusion reveals that people's sensations regarding skin moistness/roughness while rubbing their hands against each other can be dramatically altered by enhancing or diminishing certain frequency bands of the acoustic feedback arising from the same hand friction actions (see von Schiller, 1932, cited in [37,39,44,53], for an earlier demonstration of acoustic influences on the tactile sensation of roughness). This change in tactile sensations as a function of hearing has been replicated a number of times [44] but it is not easy, from current evidence, to tell apart the perceptual contributions from the more cognitive sources of this effect (just like Gescheider et al. [37,39,44,53], had pointed out earlier; see also [44] for a discussion of perceptual and post-perceptual contributions to audio-tactile interactions). That is, the question is whether the sound-induced change in the subjective ratings regarding a tactile sensation reflected a genuine change in the tactile sensation (as the authors supported), or else, if it reflected a shift in the criterion used to rate the stimuli. This shift in response criterion could arise as a consequence of expectancy biases inadvertently introduced by the method [51,78], and/or in the form of stimulus-response compatibility effects between the information conveyed by the irrelevant (sound) modality and the response required by the target (touch) modality [4,12,16,117,118].

Despite the complications involved in the interpretation of these behavioural effects, the compelling phenomenology of the demonstrations such as the ones discussed above has prompted some

research directly addressing the use of acoustic stimulation to modulate tactile sensations in applied contexts. For example, auditory cues have been found to modulate observer's judgments about crispness and staleness of certain edibles, like potato chips [120], or about the pleasantness related to the use of electric toothbrushes [122] (see [105] for a review). Some other researchers have capitalized on the tight link between audition and touch to investigate cross-modal plasticity as a consequence of sensory deprivation. For example, some authors have now reported that brain areas that are traditionally considered part of the auditory cortex (in and around the Heschl gyrus), are recruited for the processing of tactile information more strongly in congenitally deaf individuals than in hearing subjects [1,62]. A possible consequence of this plasticity is the possibility of enhanced sensitivity to touch in congenitally deaf people [61,98], an hypothesis that has led some researchers to try and use tactile aids in sensory substitution systems for deaf people [100,115,116].

4. Vibrotactile discrimination and the somatosensory system

Despite the compelling nature of the phenomenological demonstrations discussed at the beginning of previous section, and that these interactions are already being used in applied contexts, the fact is that the principles and mechanisms underlying auditory influences on tactile perception remain largely unknown. For instance, it is illustrative that in the original report of the *parchment skin illusion* [53], enhancing high frequencies of sounds inflated the ratings of roughness whereas dampening high frequencies promoted the feeling of softness, whilst in later replications [44] the direction of the effect completely reversed (see also [59], for a failure to modulate tactile texture perception with sound altogether).

One promising approach to address the mechanisms whereby acoustic input influences vibrotactile processing in the somatosensory system would be to capitalize on previous knowledge regarding perceptual discrimination tasks of vibrotactile frequency in touch. The physiological, psychophysical, and computational characterization of frequency discrimination seems to be well established for the unimodal case, at least sufficiently well to serve as a satisfactory test model to approach the cross-modal case. Embracing this approach would imply moving the primary focus of investigation away from the behavioural phenomena described above, in which participants are typically asked to make judgments about perceptual features such as roughness of surfaces, skin moistness, crispness of foods, or even perform hedonic ratings. All these tasks, albeit having a high degree of ecological validity, involve stimuli and perceptual attributes that are currently poorly understood. Even in the case of surface roughness, a texture property which has been intensively investigated, we still lack clear psychophysical and physiological characterization³ ([84,102]; see [52], for a review).

In contrast, recent neurophysiological studies provide an acceptable description of the neural correlates of perceptual comparison regarding the frequency of vibrotactile stimuli within the flutter range (5–50 Hz). In particular, Romo and co-workers [48,88–92] have studied the neural mechanisms underlying frequency

³ Although the perception of roughness may seem intrinsically related to some sort of encoding of spatio-temporal variations in the form of frequency patterns, the demonstration of this relationship has proved elusive. It seems that roughness ratings in humans depends strongly on the microstructure of the surface (the width and inter-spacing of ridges and groves) as well as on the force applied by the finger perpendicular to the surface (normal force), but appears to be largely independent of the velocity of scanning (which alters the vibratory frequency resulting from the friction; see ref. [52]).

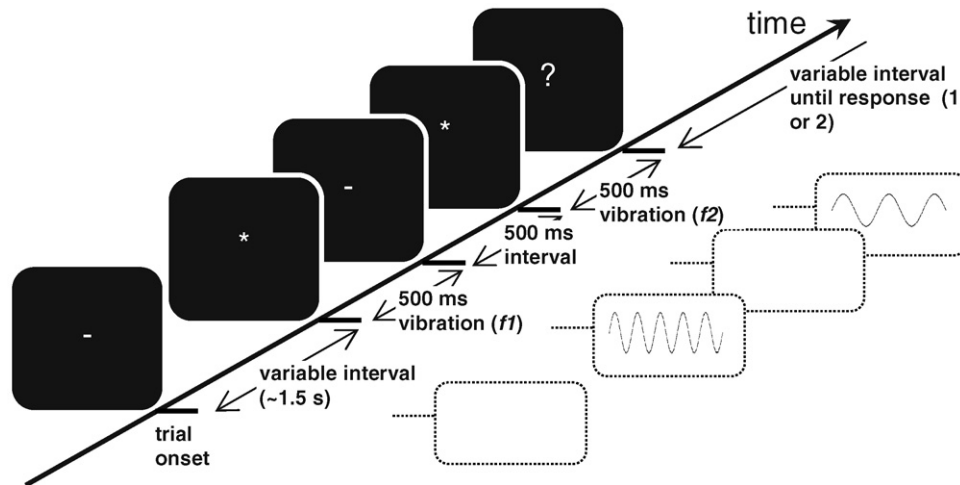


Fig. 2. Schematic illustration of the sequence of events in the frequency discrimination task (based on the paradigm used by [20]). Black boxes represent the computer screen where the participants fixated; White boxes represent the input to the vibrator placed at the participant's left annular fingertip. The task requires the participant to judge which of the two intervals contains the vibration of higher frequency. The amplitude of vibrations are previously adjusted individually so that the intensity of the sensation remains subjectively equivalent across the different frequencies used.

discrimination by measuring single-neuron and behavioural responses in monkeys trained to compare two mechanical vibrations applied sequentially to the fingertip. As in any psychophysical task, this discrimination implies a certain amount of training (both in humans and monkeys), but it has been observed that after a sharp initial improvement in performance attributable to cognitive processing (such as learning the response mapping in the task and the sequence of events in a trial), performance usually attains an asymptotic level that most likely reflects true discrimination abilities based on perceptual representations ([47]).

In the typical comparison task used in animal research, which we have recently adapted in a human experiment (see Fig. 2), a trained monkey is presented with a sequence of two brief vibrations (500 ms duration each) separated by some interval (around 1 s). The monkey has been previously trained to push one of two buttons according to whether the second vibration, f_2 , is higher or lower in frequency than the first, f_1 . Using this task, Romo and his co-workers ([91] for a review) have investigated the response properties of neurons along the various levels of the hierarchy of the somatosensory system, and have related these response properties to the input stimulus as well as to the animal's performance. They found that neurons in SI respond with a very high degree of temporal fidelity⁴ to the temporal profile of the stimulus. That is, a sinusoidal vibration of 20 Hz applied at the skin would be reflected in these SI neurons as a spike train of temporally regular bursts at approximately 20 Hz. Most neurons in SI, however, will respond only during the presence of the stimulus (activity does not persist during the inter-stimulus period), and their responses to f_2 are not modulated by the preceding stimulus (f_1). It is therefore at later stages of the network where the comparison and decision processes are to take place (e.g., the secondary somatosensory cortex [SII], the prefrontal cortex [PFC], and the medial and ventral premotor cortices [MPC and VPC]). Indeed, as one moves further down stream in the network, the temporal fidelity of the spike train response is not nearly as clear as in SI. In fact, beyond SI, the function relating

stimulus frequency and spike rate of the neuron can have either a positive or negative slope, whereas this slope is positive for most SI neurons. In addition, beyond SI, there is increasingly more neural activity during the retention period, after f_1 offset. Perhaps of particular interest is the activity of neurons in the MPC and VPC areas, the firing rate of which at f_2 presentation was found to be dependent mostly on the frequency difference between f_2 and f_1 , with the sign of that difference being a good predictor of the performance of the animal in the discrimination task. To a large extent, according to Romo et al.'s conceptualization, the cognitive process of decision making appears to be implemented in the dynamics of the whole neural network involved in the task, with some contributions to the final decision being present already in the firing rate of some SI neurons, but with the pattern of activity of neurons in the MPC and VPC playing the most dominant role.

Deco and co-workers [19,20] proposed a neurodynamical explanation of perceptual discrimination results in humans, implementing a biophysically realistic model. One interesting aspect of this model is that it reproduced the emergence of the Weber's law in frequency discrimination in a natural way. The Weber's law states that the minimum detectable change (Δx) between two stimuli depends linearly on the background intensity of the sensation (x), so that the ratio $\Delta x/x$ is a constant (so that, $\Delta x = kx + c$). This law has been extremely successful in describing human reactions to a wide range of sensory stimuli [15,27,36,50,60,76,79], but in the context of tactile frequency discrimination this is not a trivial prediction. This is because most previous demonstrations of the Weber's law have applied to variations in stimulus intensity, rather than more abstract stimulus properties such as rate of change. In fact, the results of previous research (in humans and monkeys) regarding the application of the Weber's law in frequency discrimination are mixed [40,42,66,72]; see [20] for discussion.

In particular, Deco et al. [20] explored a possible mechanism that could account for the emergence of the Weber's Law in decision making during vibrotactile discrimination. The implementation of the mechanism used a detailed spiking neural network that involved two populations of excitatory neurons engaged in competitive interactions mediated by inhibition (see Fig. 3, for a description of the model). Sensory input may bias the competition in favour of one of the populations, potentially resulting in a gradually developing decision in which neurons in the 'favoured' population exhibit increased activity while the other population is inhibited. The stable

⁴ It is perhaps important to clarify that this temporal fidelity has led to consider the hypothesis that the encoding of frequency in SI neurons is achieved directly by the timing of the spike trains. Further research has ruled out this hypothesis, showing instead that the firing rate of the neuron is sufficient to encode the frequency of flutter.

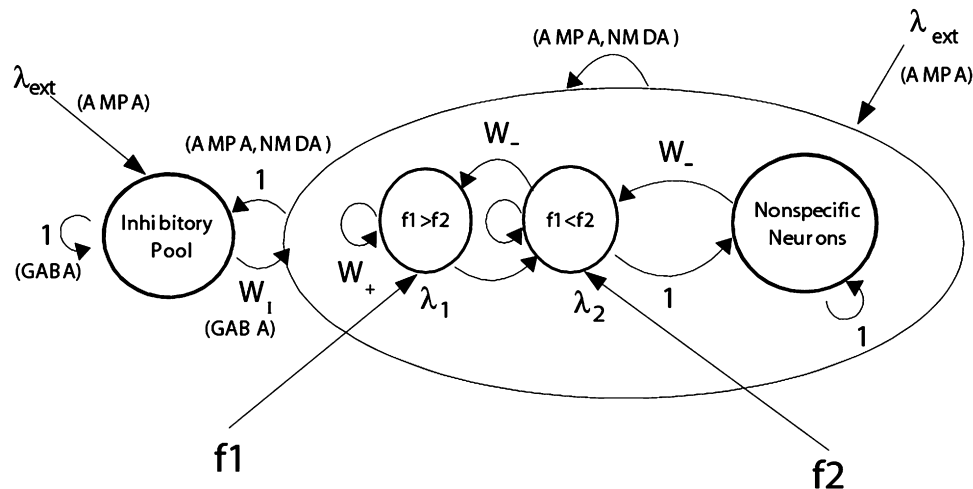


Fig. 3. The architecture of the neurodynamical model for a probabilistic decision-making network. The single attractor network has two populations or pools of neurons ($f1 > f2$) and ($f1 < f2$) which represent the decision states. One of these pools becomes active when a decision is made. If pool ($f1 > f2$) is active, this corresponds to the decision that stimulus $f1$ is greater than stimulus $f2$. There is also a population of non-specific excitatory neurons, and a population of inhibitory neurons. Pool ($f1 > f2$) is biased by λ_1 which reflects the strength of stimulus $f1$, and pool ($f2 > f1$) is biased by λ_2 which reflects the strength of stimulus $f2$. (In the simulations performed $f1$ is the frequency of the first vibrotactile stimulus, $f2$ is the frequency of vibrotactile the second stimulus, and the stimuli must be compared to decide which one has the higher frequency.) The integrate-and-fire network is subject to finite size noise, and therefore probabilistically settles into either an attractor with the population ($f1 > f2$) active, or with the population ($f1 < f2$) active, depending on the biasing inputs λ_1 and λ_2 . The network is thus a biased competition model of decision-making. The weights connecting the different populations of neurons are represented as w_+ , w_- , w_I , and 1, and their values, found after a consistent mean field analysis, are given in Deco and Rolls (2006). All neurons receive a small random Poisson set of input spikes λ_{ext} from other neurons in the system. The nonspecific excitatory neurons are connected to pool ($f1 > f2$) as well as to pool ($f1 < f2$).

states of this model were first examined using a mean-field approximation of the spiking level. For low or zero levels of input, neurons in the both populations engage in a spontaneous level of activity (~ 2 Hz). For intermediate levels of input strength, the model can settle in one of three states: the excitatory pool has either low activity, spontaneous activity or high activity. For higher levels of input, the model moves into one of two states, with the excitatory pool either having a high level of activity or a very low level. When the model is in the part of the phase state where spontaneous activity alone occurs, random fluctuations in the starting energy of the network will have little impact; the network will move into a stable spontaneous firing. When the network is in the bistable state, a small random fluctuation in its energy state will move the system into one of the stable states. In the simulations of the vibrotactile discrimination task, there was a stochastic choice as to which interval contained the target (which excitatory pool is active and which inactive). When the model is in the multistable state and its activity places it in the small energy trough corresponding to a state of spontaneous activity in the excitatory pools, then the model will not move into one of the other stable states (to decide which interval contained the target) unless activity is shifted from the spontaneous level by noise. According to this analysis, noise plays a fundamental role in the decision making process; for a network operation in the multistable part of the phase space noise is needed to shift the system into one of the required decision states.

The data arising from the simulations using the computational model described above suggested that, at least for stimulus ranges where Weber's Law holds, the underlying neural system has a multistable phase space and noise plays a critical part in decision making. This type of network performance, however, may be derived from part of the input value space and for certain degrees of learning and attention, as the relations between Δx (minimal detectable difference) and x (baseline stimulus magnitude) may change as these parameters vary (e.g., shifting performance into the bistable part of the phase space). It is worth noting, however, that the outcome of the simulations of the vibrotactile discrimination task does not necessarily imply that this analysis will characterize all perceptual

discrimination tasks, but it does highlight the role that noise may play in decision making during vibrotactile discrimination. Moreover, it illustrates how Weber's Law can be an emergent property of a system with plausible physiological properties.

5. Some relevant issues for future research

In the light of the accumulating knowledge about the unisensory processing of hearing and touch (specially the perception of vibrotactile events), there are a number of questions regarding audio-tactile interactions that would seem important and feasible to address within the context of the psychophysical, physiological and computational framework discussed above.

5.1. Levels of processing: behavioural correlates

Perhaps the most visible question around the behavioural aspect of auditory influences to vibrotactile perception is whether the actual experience of vibration at the skin can indeed change as a function of acoustic input. As discussed earlier, there are reasons to believe that the auditory-induced change of somatosensory experience is a genuine one, but previous experimental demonstrations, such as the *parchment skin illusion* [53], are subject to alternative explanations. In essence, the problem roots in that observers who are asked to rate a given property of a tactile sensation (i.e., roughness, in several of the previous experiments) have access to a concurrent acoustic event, which they are supposed to ignore, with properties that can map onto their response set. Because this irrelevant information may affect, consciously or not, decision or output processes, it is difficult to interpret the observed shift in responses as originating from a direct effect of sound on tactile experience. This type of confound is not specific to this particular audio-tactile effect nor new in the literature, and some direct analogies can be easily drawn with other areas of multisensory research involving the classical ventriloquist illusion or related phenomena [3,4,12,16,94,104]. Clarifying the contribution of sensory/perceptual versus decisional

processes to this multisensory interaction is crucial to ascertain the nature of the underlying mechanisms.

Some of the approaches that have been used to address this confound in the past involve using distractor stimuli (sounds in this case) that do not vary along the dimension being measured in the target modality (touch in this case). There are several versions of this approach: One is to find a situation in which the distractor stimulus is neutral with respect to the dimension along which the decision is made, and remains invariable throughout the experiment. If the distractor still produces an effect on judgments of the relevant stimulus/modality, then this effect cannot be attributed to its influence at the decision stage (e.g., [3]); Another approach would be to devise a distractor stimulus that varies in a form that is completely orthogonal to the set of responses that are available for the observer to use (e.g., [23,106]). A further potential strategy to address the post-perceptual confound is to use psychophysical models that allow researchers to separate the contribution of perceptual sensitivity from purely decisional effects, such as the Signal Detection Theory (e.g., [68,94]). Finally, another solution to isolate the perceptual component of inter-sensory (audio-tactile) interactions is to use an (auditory) distractor stimulus that is sufficiently intense to influence (vibrotactile) perceptual processes but weak enough so it remains undetectable to the perceiver. It is believed that, if there is no conscious perception of the distractor, then the information that it carries will not affect decisions at a conscious level (e.g., [99]).

5.2. Levels of processing: computational approach

The use of a computational approach along the lines of the one described earlier [20] may help to identify the processing level at which multisensory integration processes take place, i.e., if the integration of sounds with somatic information about vibrations is performed at higher cortical levels where perceptual decision is presumably achieved (e.g., in the case of vibrotactile detection in MPC according to, for example, [17]), or else in lower level cortical (sensory) areas where the external stimuli are initially encoded but which not necessarily support conscious perception (e.g., in the case of vibrotactile detection tasks in SI [17]). An explicit, biophysically realistic model incorporating a network system with higher and lower level cortical areas would allow addressing both types of hypothesis (i.e., integration in SI or in MPC) within the same framework. We expect a shift of the psychophysical curve corresponding to the perceptual detection of a vibrotactile stimulation as a function of the presence of auditory stimulation (a particularly interesting case is when the auditory signal is subthreshold, see behavioural approach above) if some integration takes place before or during the perceptual detection stages (i.e., MPC receives both signals or a nonlinear combination of both signals resulting from an integration in lower areas).

5.3. Levels of processing: physiological correlates

The question of the levels of processing during the auditory modulation of vibrotactile perception, which has been formulated in terms of behavioural and computational correlates above (sensory/perceptual vs. decisional processes), can be mapped in terms of the physiological correlates. Because the physiological processes related to the decision stage are supposed to occur later in time and to involve a distinct network of brain areas than the processes related to the immediate experience of an event (perception), then one would expect to find distinctive signatures in terms physiological measures. Thus, one of the most relevant questions is, How early do audio-tactile interactions occur in physiological terms? It must be clarified, however, that the term “early” is ambiguous, because

it is often used with one of two different meanings; One the one hand, we often find the word “early” associated to sensory-evoked processes that take place at a short latency after stimulus application; On the other hand, the term “early” has been also applied to processes that take place at brain structures that are functionally close(r) to the peripheral receptor system of the sensory modality being stimulated.⁵ With this distinction in mind, it is clear that the question of “How early interactions occur?” is relevant for both meanings of the term “early”, but it is important to note that the answer might not be necessarily equivalent. For example, it is conceivable that an area which is considered as being placed early in the functional architecture (i.e., primary sensory cortex) receives cross-modal modulations at a late moment in time (i.e., for example, after some neural signals have travelled to higher order association areas and were relayed back to sensory cortex). This relates to the functional architecture of the neural network implementing the multisensory integration processes, which is the question being discussed next.

5.4. Functional architecture

Another important question regarding audio-tactile interactions in vibrotactile perception relates, precisely, to the implementation of the mechanisms leading to the interactive effects being observed behaviourally. There are at least two logical architectures that have been proposed as possible implementations of multisensory interaction mechanisms in related cases (they have been briefly discussed earlier, in the context of tactile modulations in the auditory cortex). One is that the cross-modal interactions take place as a consequence of the convergence of signals during the initial inflow of information to the sensory cortices [30,54]. This type of converge would need to be supported by the presence of anatomical connections between brain structures at functionally early stages of the sensory pathway. Some reports have revealed the existence of such connections between the visual and auditory cortices [25,85] and between tactile and auditory cortices [33] which could embody early interactions. What has not been established yet is whether these anatomical connections do play a causal role in the interactions being reported in functional studies. Even if these connections were to play a role in some behaviours, however, it is likely that they cannot explain all cases of cross-modal interactions. This brings us to the second type of functional architecture, which is that of recurrent connections. That is, (at least) some of the cross-modal interactions potentially addressable between modalities, including the particular case of hearing and touch, can be supported by feedback from association areas to the sensory cortices. That is, in a simple version of this type of model, a first sweep of activity would carry information independently along to the particular ascending pathways corresponding to the sensory stimuli being processed, which would later converge onto higher order (association) regions of the cortex, and finally revert back in the form of a modulatory signal onto (functionally early) unisensory areas.

There is evidence of massive interconnectivity in the brain, including the fact that for the most part, when two brain structures are connected they are so by means of bidirectional connections [28]. From this evidence, as well as because of the pervasive effects that higher level cognitive processes (such as attention) can exert on low level sensory processes, be them cross-modal [65] or uni-modal effects [58,109], one would need to concede that recurrent connec-

⁵ The question of timing and brain localization of multisensory processes has been frequently investigated in various previous studies, in special for the case of tactile modulations of auditory processing. These have been discussed earlier in this manuscript.

tions are to play a role in the outcome of multisensory interactions. The question is, therefore, not whether one or the other type of architecture is, in general, the basis of multisensory integration effects, but to which degree a particular multisensory integration process can be attributed to feed-forward convergence mechanisms. Thus, it appears to be important to investigate the type of architecture supporting the auditory modulations of vibrotactile processing in its own terms.

5.5. Specificity

A further question refers to how attribute-specific multisensory (or in particular, audio-tactile) interactions are. This question is starting to prove relevant in the case of some multisensory interactions reported in the past, especially those occurring at very short latencies (registered with electrophysiological measurements in humans and animals), because the answer can help to characterize the underlying mechanisms [21]. In particular, the question is if the modulatory effect of one modality on another is constrained by whether the information contained the two modalities is coincident in some stimulus attribute/s or not (i.e., spatial location, motion direction, semantics, etc.). Answering this question for a particular type of multisensory interaction may be informative as to the characteristics of the modulatory signal, and therefore, as to the source of this modulation in the network.

In general, there are several stimulus attributes that can be of potential interest to test specificity, especially those that can be encoded in more than one sensory modality, such as for example spatial location. In fact, despite the apparently robust finding of spatial specificity in some multisensory interactions (such as those between visual and auditory processing, in neurons of the SC in animals; [107,108]; and [32]; for evidence in human behaviour), there are other examples involving sound and touch which seem to point to a different conclusion [41,73]. Indeed, recent studies suggest that spatial specificity of audio-tactile interactions might be found in some parts of space but not others (i.e., rear vs. front) [56,26]), for some body parts and not others [110] and even depend on the particular individual being tested [77]. Another potentially important aspect regards the kind of auditory stimuli used, given that audio-tactile interactions are stronger for complex stimuli [56,26]. One particularly relevant example, discussed earlier, is the lack of spatial specificity of auditory masking of tactile stimulation reported by [41,73]. In that case, this lack of specificity led the authors to interpret that the auditory influence on tactile detection arose from a global inhibitory influence from subcortical structures. In the context of acoustic modulations of vibrotactile processing, an interesting test of specificity would be to check whether the auditory influence of tactile perception is frequency specific of not (see [119], for initial evidence).

6. Concluding remarks

In this article we have attempted to persuade the reader about the relevance of studying auditory contributions to vibrotactile perception as a mean to address several relevant aspects of multisensory integration. First, we have pointed out the close relationship between the type of encoding of vibrotactile events at the skin and the ear. In the first place, the sensitive ranges for vibrations in both senses overlap, and in consequence, there is opportunity for interactions of an integrative nature right from the initial stages of information processing. Second, we have discussed several behavioural manifestations of audiotactile interactions in the domain of frequency, such as the *parchment skin illusion* and other related phenomena where the reports about feelings of roughness

at the skin are dramatically altered by concurrent sounds. Despite the fact that these phenomena are starting to echo in the form of real world applications, we are still in the dark about the actual underlying mechanisms. Recent work about tactile and auditory processing, and especially physiology and neuroimaging literature looking at audio-tactile interactions in the auditory cortex can be of interest as a guide to address this question. We believe that advancing in the knowledge about the cerebral and cognitive mechanisms underlying the multisensory contributions to vibrotactile perception will require the adoption of a robust psychophysical paradigm, such as the one used in somatosensory research for frequency discrimination tasks, which allows researchers to combine psychophysical, computational and physiological approaches.

In the last section of the article, we have highlighted several research questions that potentially addressable using the psychophysical framework proposed above, and that are of general interest to multisensory research. These questions are articulated around the nature of the robust phenomenology of the *parchment skin illusion* and related phenomena. In particular, we have examined the ramifications of this question in terms psychophysics, physiology and computational modeling. We have also highlighted the relevance of the functional architecture of the brain networks supporting potential audio-tactile interactions, and in particular of the relative roles of interactions at the level of initial feed forward connections versus those enabled by feedback loops. Finally, we have also brought up the question of specificity of potential audio-tactile interactions in terms of stimulus properties, an issue which can prove highly informative for several of the questions posed earlier, and in particular about the functional architecture.

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