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TACTILE PERCEPTION – PERCEPTION OF TACTILE DISTANCE ON A SINGLE SKIN SURFACE CHANGES WITH STIMULUS ORIENTATION: A NEURONAL NETWORK MODELLING STUDY

Tesi di Laurea in:

Sistemi Neurali LM

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… To the people who make my London experience much better than an amazing dream …

… We are too concerned with what was and what will be …

There’s a saying:

Yesterday is history,
Tomorrow is a mystery
But
Today is a gift.
That is why it’s called PRESENT.

Keywords:

- Computational Model
- Synaptic Connections
- Tactile Perception
- Weber’s Illusion
- Anisotropy

Index

Introduction

Interaction between the environment and us occurs through any kind of external stimuli (tactile stimuli, visual stimuli, acoustic stimuli, etc.) we receive as well as their elaboration. The brain provides this special ability, which is also a result of our experience.

Sometimes integration and elaboration of inputs coming from the environment may produce illusion.

This occurs, for example, in case of tactile perception. In fact, perception of tactile distances changes with body site. The concept that distance on the skin is frequently misperceived, was first discovered over a century ago by Weber. Perceived distance is larger on regions of high tactile sensitivity than over those with lower acuity. The effect is now known as *Weber's illusion*. Besides this illusion, another important phenomenon observed in vivo is that perceived distance depends on the stimuli orientation. In other words, perception of tactile distance over a skin surface changes with stimulus orientation.

Recently, Longo and Haggard [Longo & Haggard, J.Exp.Psychol. Hum Percept Perform 37: 720-726, 2011]– in order to investigate how body shape is coded within the brain - compared tactile distances presented in different orientations on the hand. They found that distances between two punctual stimuli applied *across* the hand are consistently perceived larger than the same distances applied *along* the hand. This illusion is known as Orientation-Dependent Tactile Illusion and some results in the literature provide evidence that the extent of this illusion also depends on the applied distance. In fact, Green in his paper (Green, Percpept Pshycophys 31, 315-323, 1982) evidenced that the greater is the applied distance the greater is the orientation-dependent tactile illusion.

Weber’s Illusion and orientation-dependent tactile illusion are generally explained in the literature considering differences in receptor density, differences in dimension and shape of receptive fields (RFs), and cortical magnification effects in the primary somatosensory cortex (SI) (i.e., different extents of somatosensory cortex are allocated for different body regions)

Anyway, the explanation based only on differences in receptor density, RF’s shape, and cortical extent in SI is unsatisfactory as orientation-dependent tactile illusion is smaller compared to the effect that the previous cited differences would produce. This suggests that tactile information, behind primary somatosensory cortex, receives further processing in higher cortical areas that may operate a sort of “rescaling process” acting in order to reduce the gap of judgment in terms of distance perceived in different orientations, and to preserve tactile size constancy.

The neural mechanisms and neural circuits acting in the brain to produce rescaling are still largely unknown. Aim of the present work is to gain insight into this particular aspect of tactile perception (orientation-dependent tactile illusion) by means of a neural network model.

The main hypothesis included in this work is that tactile information is processed at two different levels, corresponding to two different neural layers. One of them represents a lower-level layer (called Area1) in which a first and distorted tactile representation is created. This layer may mimic the primary somatosensory area, where tactile distance representation can be significantly distorted depending on stimuli orientation and skin surface, because of differences in RFs’ size and shape and cortical magnification. The other one (called Area2) represents a higher-level layer that receives the distorted information from the previous layer and reduces this distortion by rescaling tactile information toward their true size. This layer may correspond to superior cortical areas (e.g. in the temporal or parietal cortex) that are recruited in distance judgment and implicated in the rescaling process. In the model, neurons within Area1 receive information from the external space (skin) and send information to neurons within Area2 via feed-forward synapses. Furthermore, neurons with each area communicate via lateral synapses: lateral synapses provide an important contribution for the elaboration of the external stimuli.

It is worth noticing that the developed model is mainly a conceptual model and it does not aspire to an accurate reproduction of the physiological and anatomical structures. So, I focused on an abstract level of implementation, without specifying an exact correspondence between layers in the model and anatomical brain regions. Anyway, the mechanisms included in the model are biologically plausible.

Hence, the neuronal network could be helpful for a better understanding of the several mechanisms that operate within the brain in order to elaborate tactile inputs. In fact, the model is able to simulate several results both of Longo & Haggard’s paper as well as Green’s paper.

The present Thesis is organized as follows.

Chapter 1 includes a review of the more relevant results of the neurophysiological and psychological literature that have been used for model implementation and validation. Chapter 2 provides an accurate description of the developed neural network: it includes a description of network architecture, contains all the mathematical formulas, and provides explanation of model parameters. Chapter 3 presents all neural network results together with their analysis and interpretation. Finally, in Chapter 4 sensitivity analysis on model parameters has been conducted to test the robustness of the model against variation in some key parameters.

The main part of the dissertation project was developed at the Department of Psychological Sciences of the Birkbeck University of London, under the supervision of Dr. M. Longo. In particular, Dr. Longo helped me in the implementation of the neuronal network, in the interpretation of model results as well as in the their validation.

This experience also offered me the possibility to improve my knowledge concerning neurosciences. Moreover, this experience in London was the first one abroad for me and it gave me the possibility to improve my English, to make a lot of new friends coming from other country and being more self-confident.

Chapter 1

Touch and Perceived Distance: State of the art

My dissertation project consists in the implementation of a computational model that reproduces a particular aspect of tactile information processing, that is how the brain elaborates touch information coming from a skin surface of the body. In particular, I focused on how the brain could reproduce perceived distance as a function of the orientation of two stimuli applied on a specific skin region (dorsum of the hand).

It is known that the perceived distance between two stimuli applied on a skin surface is judged different from region to region of our body.

The concept that distance on the skin is frequently misperceived, was first discovered over a century ago by Weber. Weber and others have reported that the apparent distance between two pressure stimuli fluctuates with both body site and stimulus orientation. In particular, it is larger on regions of high tactile sensitivity than on those with lower acuity. This effect is known as *Weber's illusion*.

This illusion suggests that tactile size perception involves a representation of the perceived size of body parts preserving characteristics of the somatosensory homunculus.

It is well known that somatosensory homunculus shows a representation of how much of somatosensory cortex innervates certain body parts.

Moreover, it seems Weber's illusion doesn't exist only on different regions of the body but also considering different orientation over the same skin surface. In fact, Matthew Longo and Patrick Haggard of the Institute of Cognitive Neuroscience (University College London), made an experiment in which they investigated how the tactile perception on the dorsum of the hand can be affected by the orientation of two stimuli applied over the skin. They found that the perception of the two points distance is larger across the hand (medio-lateral direction) rather than along the hand (proximal-distal direction).

This suggests the existence of orientation anisotropies of both tactile acuity and of tactile receptive fields (RFs) of cortical neurons. So, shape of tactile RFs may partly explain distortions of mental body representations.

In addition, the paper "*The perception of distance and location for dual tactile pressures*" written by Barry G. Green of the Princeton University in New Jersey, reports similar conclusion and provides further information about this effect.

Anyway, differences in tactile perceived distance across different skin regions of the body and/or different orientations on a specific skin area are not as high as expected simply by looking at the sensory homunculus.

This suggests that tactile information, behind primary somatosensory cortex, receives further processing in higher cortical levels that acts in order to reduce the gap of judgment in terms of distance perceived in different body parts or different orientations.

The effect is known as *rescaling*. However, the neural mechanisms acting in the brain to produce rescaling are still largely unknown.

Aim of the present work is to gain insight into this particular aspect of Weber's Illusion by means of a neural network modelling.

Of course, the model represents an approximation of the behaviour of different cortex levels considering several simplifications.

Before giving an accurate explanation of how the model works, I will present several results of the neurophysiological and psychological literature that have been accounted for in model implementation and model behaviour.

Somatosensory system

The somatosensory system is composed of the receptors and processing centres that produce the sensory modalities such as touch, temperature, proprioception (body position), and nociception (pain). The sensory receptors cover the skin and epithelia, skeletal muscles, bones and joints, internal organs, and the cardiovascular system. While touch (also called somatosensory) is considered one of the five traditional senses, the impression of touch is formed from several modalities. In fact, the term touch is often replaced with *somatic senses* to better reflect the variety of mechanisms involved.

The system reacts to diverse stimuli using different receptors: thermoreceptors, nociceptors, mechanoreceptors and chemoreceptors. Transmission of information from the receptors passes via sensory nerves through tracts in the spinal cord and into the brain. Processing primarily occurs in the primary somatosensory area in the parietal lobe of the cerebral cortex.

At its simplest, the system works when activity in a sensory neuron is triggered by a specific stimulus such as heat; *this signal eventually passes to an area in the brain uniquely attributed to that area on the body; this allows the processed stimulus to be felt at the correct location*.

Hence, the interaction between our body and the environment involves a complex process that the somatosensory system executes in order to obtain the best output it needs to interact with the environment itself. Therefore, it is important to explain any single step of a tactile stimulus processing.

Mechanoreceptors and Receptive Fields in the skin

Mechanoreceptor in the skin mediate touch, so the higher is the number of mechanoreceptor in a specific skin region, the higher is the tactile sensitivity. For example, tactile sensitivity is higher on the hairless (glabrous) skin on the palmar surface of the hand rather then on the dorsum. In general, tactile sensitivity is greatest on the hairless skin on the fingers, the palmar, the sole of the foot and the lips.

Glabrous skin is characterized by regular array of ridges formed by folds of the epidermis. Each ridge contains a dense matrix of mechanoreceptors, which mediate the sense of touch. In fact, any time there is a motion over the skin surface or an indentation on it, they excite. The depth of the indentation depends on the force exerted by the object on the skin as well as on its dimension and shape.

All mechanoreceptors sense these changes in skin contour but differ morphologically in important ways that affect their physiological function.

Thanks to histological and physiological studies it is now clear there are four major types of mechanoreceptors in glabrous skin. Two of these are located in the superficial layers of the skin (Meissner's corpuscle and Merkel disk receptor) and two are situated in the subcutaneous tissue (Pacinian corpuscle and Ruffini ending). The small superficial receptors sense deformation of the papillary ridges in which they reside. The larger subcutaneous receptors sense deformation of a wider area of skin that extends beyond the overlying ridges [***ref. 1***].

Moreover, these types of mechanoreceptors have different Receptive Fields (RFs) that play an important role in the processing of any stimulus.

A receptive field is a region of the skin from which a sensory neuron is excited. The size and structure of receptive fields differ for receptors in the superficial and deep layers of the skin. In fact, receptors in the superficial layers on the skin resolve fine spatial differences because they transmit information from a restricted area of skin. This very fine resolution allows humans to perform fine tactile discrimination of different surfaces.

Conversely, mechanoreceptors in the deep layer of the skin sense more global properties of objects and detect displacement from a wide area of the skin [***ref. 2***].

In addition, variation in receptive fields size has been to consider as an important factor that reflects the density of mechanoreceptors in the different regions of the skin. That is, spatial resolution of stimuli applied over the skin surface depends on density of mechanoreceptors, which varies throughout the body. This is represented in *Figure 1*.

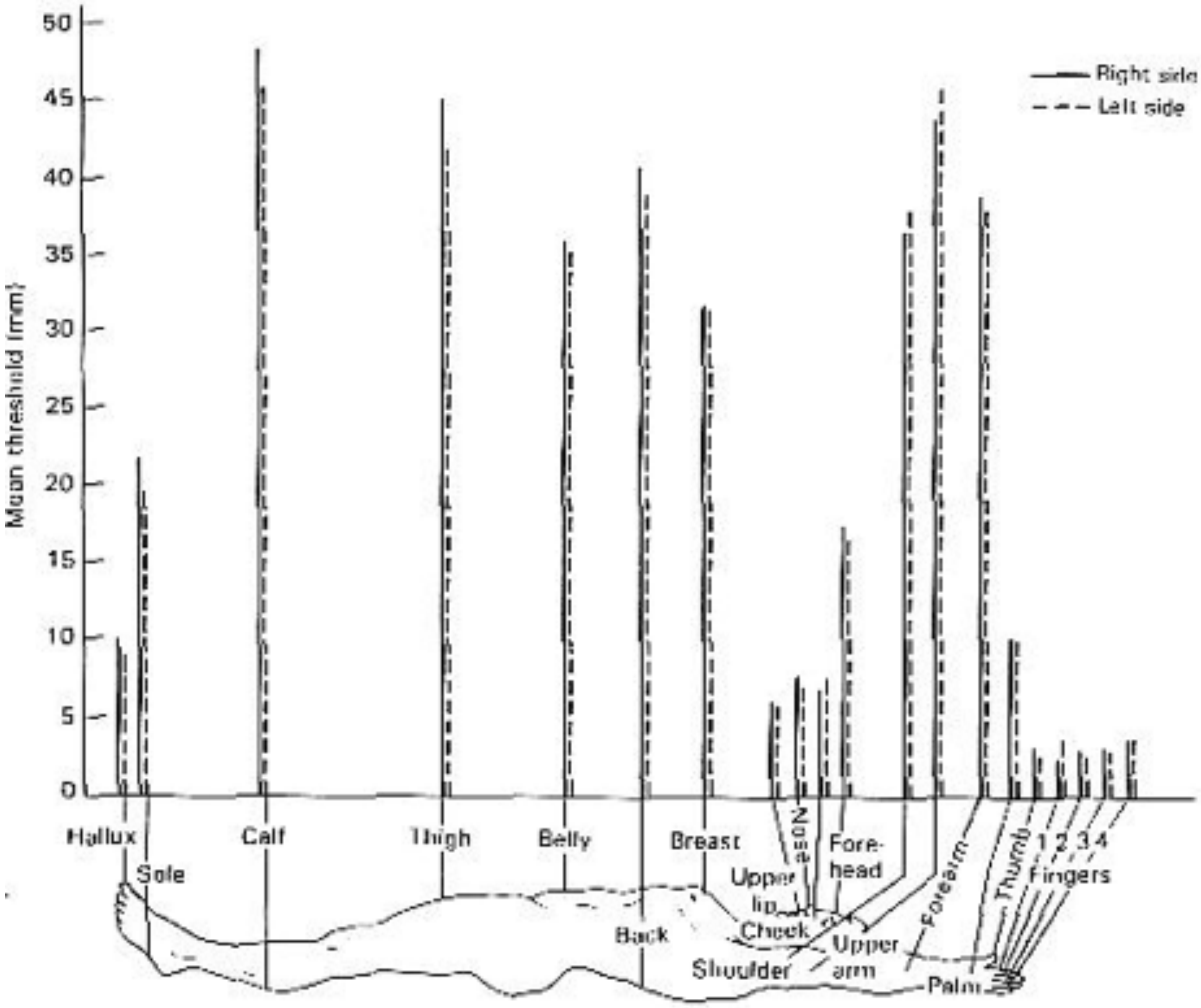


Figure 1. Spatial resolution of stimuli varies throughout the body surface.

In other words, the size of the receptive fields in a particular region of the skin establishes the capacity to determinate whether one or more points are stimulated. So, if two points within the same receptive field are stimulated, the sensory neuron innervating mechanoreceptors within this RF, will elaborated them as single continuous sensation which spans the distance between the points.

Instead, if the points are located in the receptive fields of two different nerve fibres, the information about both points of stimulation will be signalled. The minimum distance between two detectable stimuli is called the *two-point discrimination threshold*. The two-point discrimination threshold varies from body region to body region and it depends on the size of the receptive fields and the innervation density of mechanoreceptors in the superficial layers of the skin.

Anyway, any information gathered by each mechanoreceptor is transmitted by sensory neurons to the spinal cord as well as the brain. These sensory neurons are called *Dorsal Root Ganglion Neuron*.

Dorsal Root Ganglion Neuron

As I wrote before, all somatosensory information from the limbs and trunk is conveyed by dorsal root ganglion neurons. In particular, each neuron is well suited to its two principal functions:

- *Stimulus transduction.*
- *Transmission of encoded stimulus information to the central nervous system.*

We can roughly think that this neuron is composed by a central body sitting in a ganglion on the dorsal root of a spinal nerve and an axon divided into two branches. One of them is linked to mechanoreceptors in the skin and the other one projects to the central nervous system.

As Dorsal Root Ganglion Neuron transmits encoded stimulus information to the spinal cord or brain system, is usually renamed *primary afferent fibre*.

See the picture below for a better understanding.

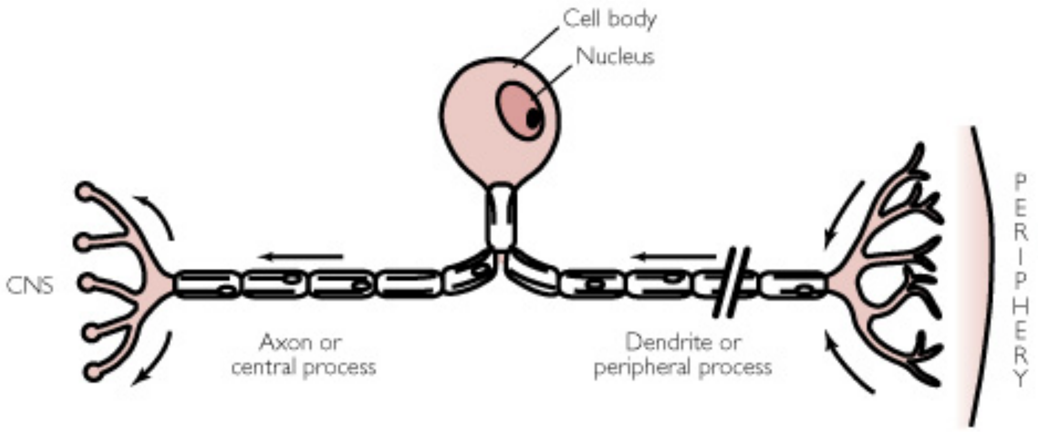


Figure 2. Dorsal Root Ganglion Neuron.

The primary afferent fibre performed two different classes of somatic sensation such as *Epicritic sensations* and *Protopathic sensations*.
The first class involves fine aspects of touch for example the ability to detect gentle contact of the skin, localize the stimulated position of the skin and resolve spatial details. The second class involves pain and temperature senses. The present work does not consider protopathic sensations.

Somatic Sensory Cortex

Information transmitted to the brain from mechanoreceptors enables us to feel the shape of objects and get other further information about them such as their specific dimensions.
How could we get all this further information by simply touching an object with our fingers for example? In this chapter I will try to reply.
First of all, any information mechanoreceptors on the skin are able to get, is convey to the brain thanks to sensory neurons. So, information should be integrated inside the brain in order to achieve a final output such as dimensions features of objects we have touched. But, how does cerebral cortex integrate and transform sensory information coming from the periphery? How the cortex constructs an image of objects we touch from the fragmented information provided by the

receptors of the skin?

The ability to recognize objects placed on the hand on the basis of touch alone is one of the most important and complex functions of the somatosensory system.

It is known that tactile information about an object is fragmented by peripheral sensors and must be integrated by the brain. In fact, many familiar objects such as an apple, a screwdriver or a set of keys are much larger than the receptive field of any receptor in the hand. These objects stimulate a large population of sensory nerve fibres, each of which scans a small portion of the object. The peripheral sensory apparatus deconstructs the object into tiny segments because Dorsal Root Ganglion Neurons convey information from only a small area of the receptor sheet. When a particular nerve fibre fires an action potential, it signals that its territory has been contacted at intensity sufficient to cause it to fire. *By analysing which nerve fibre has been excited, the brain reconstructs the pattern made by the object.*

So, several nerve fibres convey tactile information to the cortex providing many parallel pathways to the brain. It is the job of the central nervous system to construct a coherent image of the object from fragmented information coming from multiple pathways. In particular, a big contribution is given by *Somatic Sensory Cortex*. It consists of three different major divisions: *Primary Somatic Sensory Cortex (S-I), Secondary Somatic Sensory Cortex (S-II), Posterio Parietal Cortex*. S-I is divided into four different areas: *Broadmann's areas 3a, 3b, 1 and 2*. These four regions of the cortex differ functionally. Areas 3b and 1 receive information from the mechanoreceptors in the skin, whereas areas 3a and 2 receive proprioceptive information from receptors in muscles and joints. However, the four areas of the cortex are extensively interconnected, so that both serial and parallel processing is involved in higher-order elaboration of sensory information.

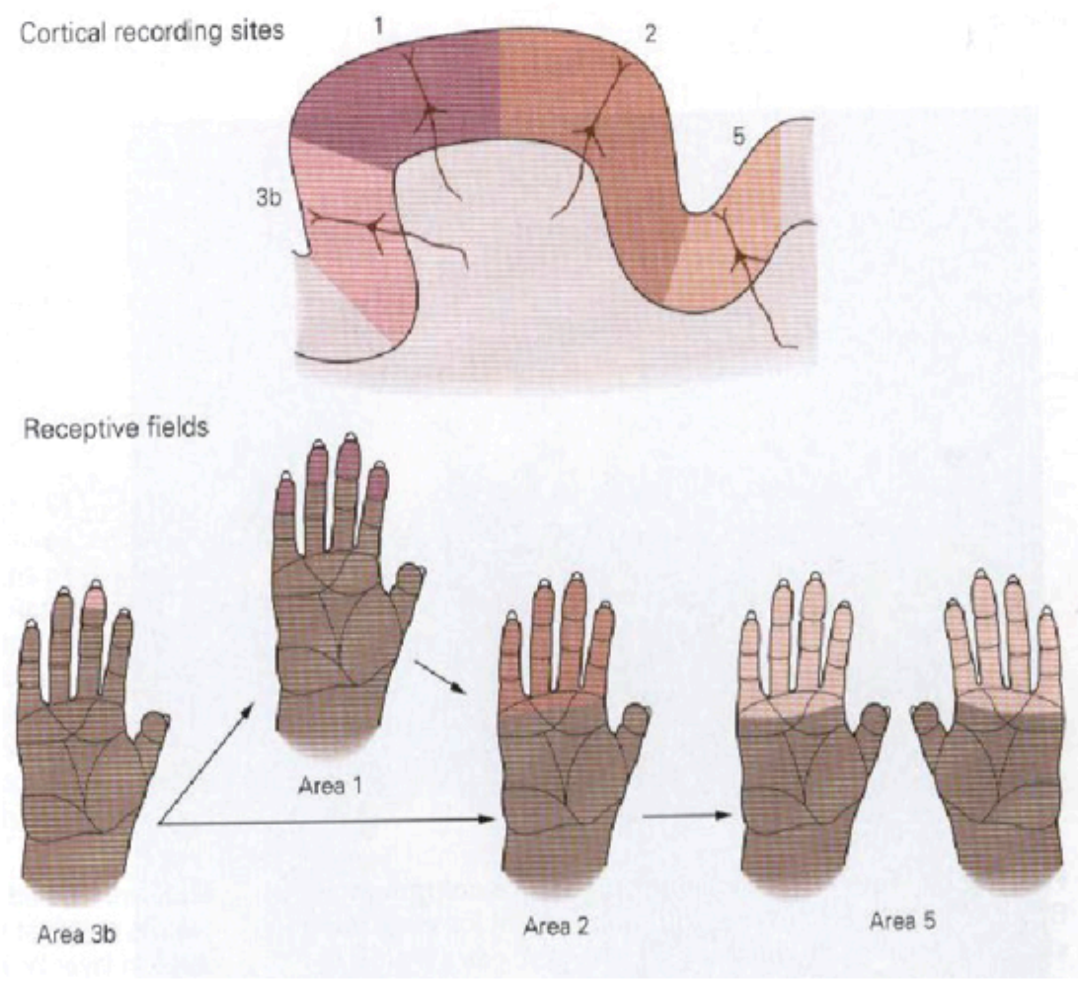
S-II is innervated by neurons from each of four areas of S-I. The projections from S-I are required for the function of the S-II. For example, when the neural connections from the hand area of S-I are removed, stimuli applied to the skin of the hand do not activate neurons in S-II.

Finally, other important somatosensory areas are located in the Posterior Parietal Cortex (Brodmann's area 5 and 7). These areas receive input from S-I. Area5 integrates tactile information from mechanoreceptors in the skin with proprioceptive inputs from the underlying muscles and joints. This region also integrates information coming from the two hands. Area 7 receives visual as well as tactile and proprioceptive inputs, allowing integration of visual information.

Since each cortical neuron receives inputs from receptors in a specific skin area, central neurons also have receptive fields. Thus, each cortical neuron is defined by its receptive field as well as by its sensory modality. *Any point in the skin is represented in the cortex by a population of cortical cells connected to the afferent fibres that innervate that point on the skin.* When a point on the skin is touched, the population of cortical neurons connected to the receptors at that location is excited. Stimulation of another point on the skin activates another population of cortical neurons. *We perceive contact at a particular location on the skin because a specific population of neurons in the brain is activated.*

It is important to say that RFs of cortical neurons are much larger than those of dorsal root ganglion neurons. For example, the RFs of sensory neurons innervating a finger cover tiny spots on the skin, while those of the cortical cells receiving these inputs are large areas covering an entire fingertip, or several adjacent fingers, or the palmar surface of the contralateral hand.

For a better understanding see *Figure 3*.



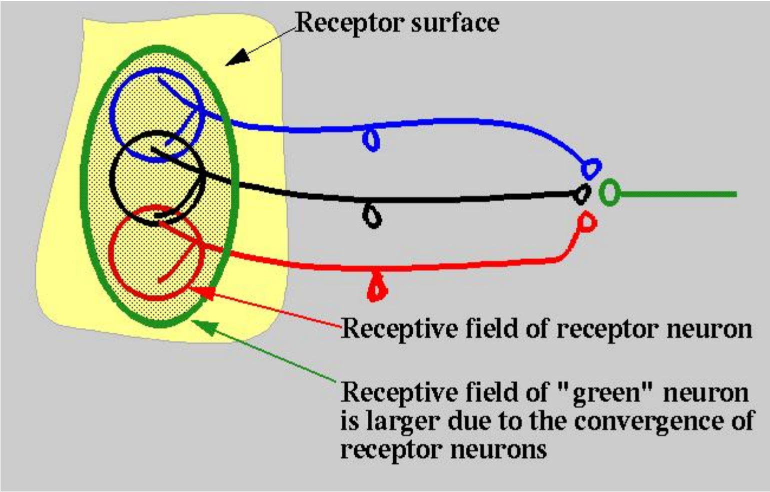


Figure 3. The receptive fields of neurons in the Primary Cortex are larger than those of the sensory afferents.

The size and the position of cortical receptive fields on the skin are not fixed permanently but can be modified by experience or by injury to sensory nerves. For example a tennis champion will develop a larger proportion of cortical neurons devoted to sensory input on the arm than a pianist, who needs a larger proportion of cortical neurons devoted to sense inputs coming from each finger.

Although the RFs of cortical neurons cover a large area of the skin, a cortical neuron is nevertheless able to discriminate fine detail because it responds best to excitation in the middle of its receptive field. Thus, a stimulus applied to the tip of the finger strongly excites some neurons, while others fire weakly or not at all. If a more proximal spot on the finger is touched, many of the same cells are activated but in different proportions. Information provided by the entire population of excited cells localizes a stimulus on the skin. The somatotopic arrangement of somatosensory inputs in the human cortex is called *homunculus*. *This is not more than a visual representation of the concept of "the body within the brain" that one hand or face exists as much as a series of nerve structures or a "neuron concept" as it does a physical form.*

However, the internal representation of our body does not duplicate in a correct way the spatial topography of the skin. In fact, the images of the body in the brain exaggerates certain body regions such as hands, feet, mouth and compress other regions such as trunk, arms and so.

The reason for the bizarre, distorted appearance of the homunculus is that the amount of cerebral tissue or cortex devoted to a given body region is proportional to how richly innervated and sensitive that region is, and not to its size. The homunculus is like an upside-down sensory map of the contralateral side of the body.

It is easy to understand that somatosensory homunculus is represented by huge hands, lips and face in comparison to the rest of the body because there are a lot of sense nerves in these specific regions. Those regions are important sensor of the properties of objects and thus have the highest density of tactile receptors.

Instead, the proximal portions of the limbs and trunk are much less densely innervated; correspondingly, fewer cortical neurons receive inputs from these regions.

An important consequence of the magnification of the hand representation in the cortex is that the size of individual peripheral receptive fields on the hand covers a much smaller area of skin than receptive fields on the arm, which are smaller than receptive fields on the trunk. The figure below gives us an illustration of the sensory homunculus.

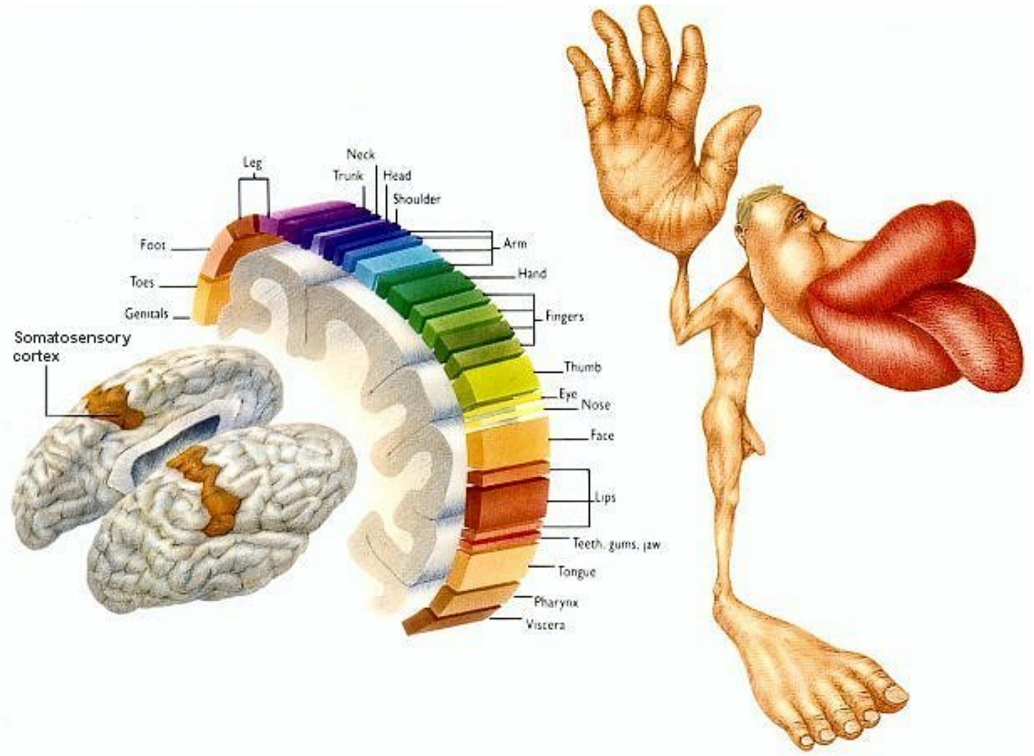


Figure 4. Sensory Homunculus is an original model of our body. Each part of the Somatosensory cortex is dedicated to a specific body region.

Another important phenomenon has to be considered in order to explain the spatial resolution within the sensory cortex. In fact, it not depends only on the innervation density over the skin but also on how cortical neurons could communicate each other. As I wrote before, when a particular stimulus is applied on a certain point of the skin, cortical neurons with RFs covering that position will activate, increasing their firing rate (a population of neurons will be activated). However, if many neurons are activated at the same magnitude, the spot represented by the stimulus could be blurred and the position of it will not be identified in the best way by the brain. In order to find out the best localization, cortical neurons interact to each other not only via excitatory synapses but also with inhibitory ones. That is, if a neuron is activated it will tend to excite proximal neurons nearby and inhibit more distal ones. In other words, stimulation of regions of skin, surrounding the excitatory region of the receptive field of a cortical neuron, may reduce the responsiveness of the neuron to an excitatory stimulus because afferent inputs surrounding the excitatory region are inhibitory.

It is now clear that inhibitory interactions are particularly important for fine tactile discrimination. In fact, if two stimuli applied on a skin surface are very close, the activity of both populations will overlap each other and the distinction between the two peaks might become blurred. However, the inhibition produced by each stimulus also summates in the zone of overlap. As a result of this more effective inhibition, the peaks of activity in the two responding populations become sharpened, thereby separating the two active populations spatially. What I have just explained might become clearer by having a look at the figure below.

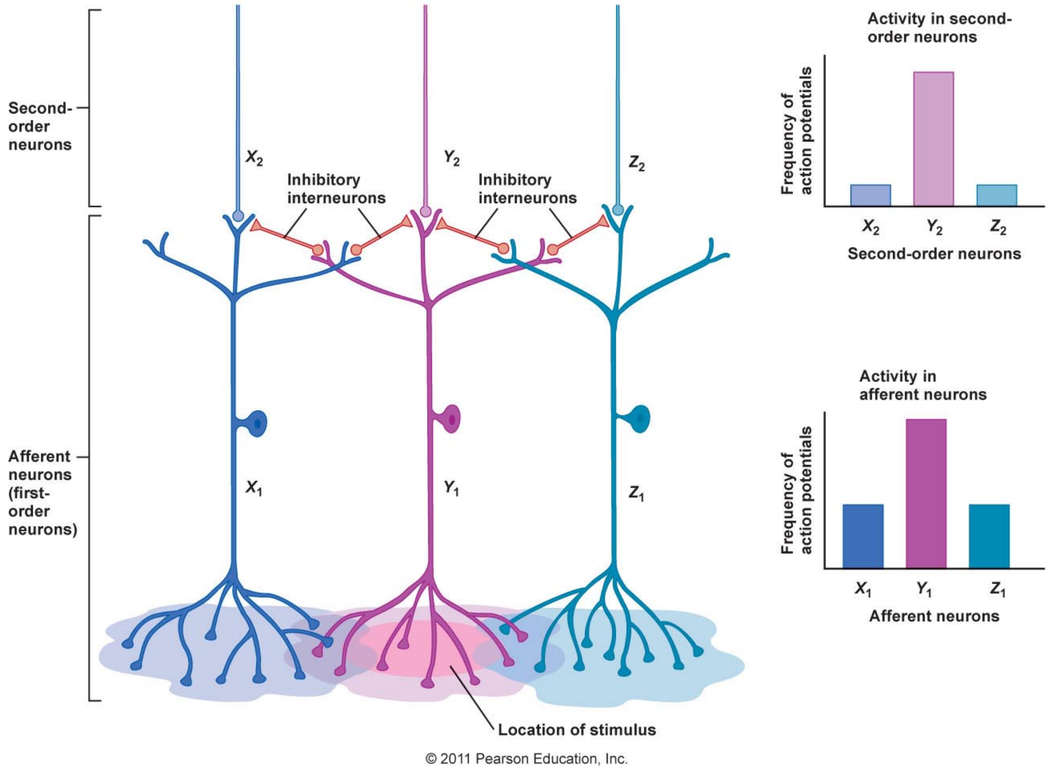


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Figure 5. Surround inhibition. Inhibitory interneurons provide a better localization of the stimulus, as there is a greater discrimination between the activities of the second-order neurons. Note that the activation of X_1 and Z_1 is higher than the activation of X_2 and Z_2.

WEBER’S ILLUSION: what is it and why does it exist?

Although inhibitory synapses between neurons might figure out the discrimination of two stimuli very close to each other, it is not always true that the perceived location of the stimuli and the perceived distance between them correspond to the real physical position and distance of the two stimuli. That is, perceived distance often differ by the physical one. Moreover, perceived distance differs from body region to body region because of sensory acuity changes with skin surface.

In other words, supposing to apply two punctual stimuli on the hand of a subject at a certain distance and then to apply the same stimuli on the arm of the same subject and at the same distance, *subject will perceive a larger distance on the hand than on the arm*.

How is it possible?

The real distance is the same but it is judged as not as the same.

Weber has detected this sort of tactile illusion and that is why it is called *Weber's Illusion*.

In 1834 E. H. Weber described accurately that when compass-points, kept equidistant, are moved with equal pressure over a cutaneous surface of varying sensitivity, the observer experiences a converging or a diverging of the two paths; a converging, when the points pass from an area of greater to one of less sensitivity, and a diverging when they pass from an area of less to one of greater sensitivity. Weber indicated, in some detail, the form of the illusion as found at twelve different regions of the body.

After Weber's work, other studies have been conducted in order to discover more about Weber's Illusion as well as if it might appears in different ways.

Interesting results were obtained. In fact, it seems that this sort of tactile illusion is present not only by comparing different body regions but also analysing a specific skin surface by changing the orientation in which stimulation was applied. Further information could be find by taking a look at Matthew R. Longo and Patrick Haggard's Paper, "*Weber's Illusion and Body shape: Anisotropy of Tactile Size Perception on the Hand*".

They investigated how body shape is coded within the brain, by comparing tactile distances presented in different orientations on the hand. In particular, the authors applied two punctual stimuli on the hand; in same cases the distance between the two stimuli was oriented along the hand, in other cases the distance between the two stimuli was oriented across the hand. Longo and Haggard found that across (medio-lateral axis) distances are consistently perceived as larger than along (proximo-distal) ones. This is completely true if the experiment is conducted over the dorsum of the hand. A second experiment reveals there is not as such as good discrimination between across and along distances on the palm of the hand. In other words, Weber's Illusion could change at any skin region of the same body part [***ref. 3***].

In Longo & Haggard experiment, participants made un-timed two-alternative forced-choice judgments of whether the two points felt farther apart in the along or across orientation, and responded verbally.

There were five pair of stimuli, according to the size of the transverse and longitudinal orientation (across/along): 2/4 cm, 2/3 cm, 3/3 cm, 3/2 cm, 4/2 cm. Stimuli were applied approximately on the centre of the dorsum of the hand.

Each ratio was applied 14 times for each of twenty participants. So, the total trials number was 70.

The proportion of trials in which the ‘across’ stimulus was judged as larger was analysed as a function of the ratio of the length of the along and across stimuli, plotted logarithmically to produce a symmetrical distribution about the point-of-actual-equality (i.e., ratio equals to 1).

Figure 6 (Figure 3 Normal Case, Longo & Haggard Paper), clearly demonstrates when the ratio is equal to 1, transversal sizes are judged larger than longitudinal sizes. Investigated distances are judged equal to each other if a ratio lower than 1 is provided.

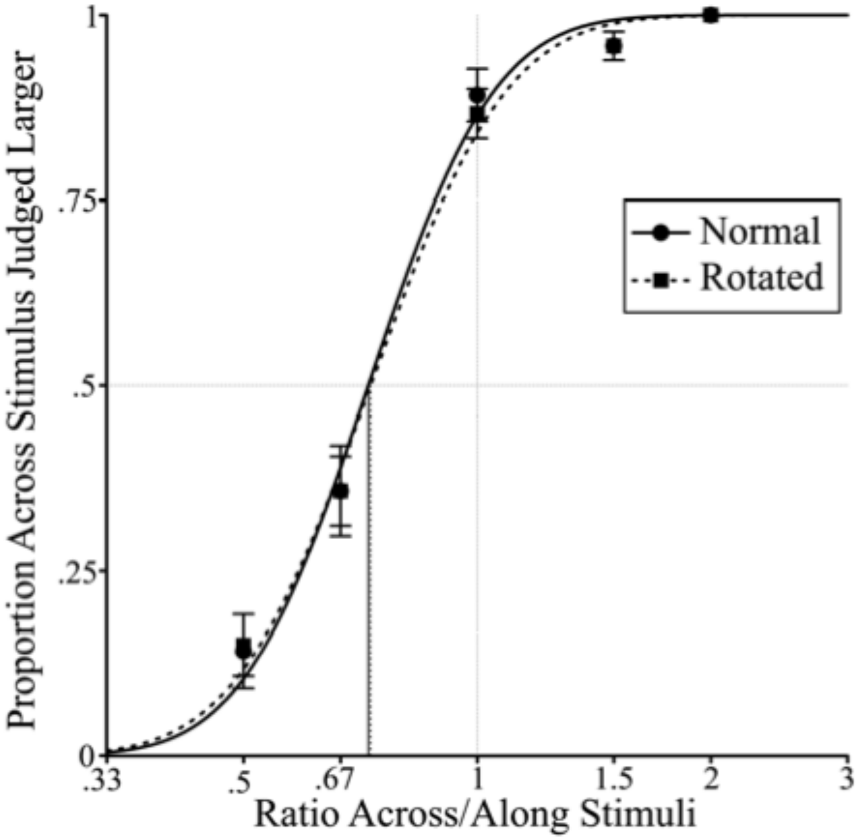


Figure 6. Proportion Across Stimulus Judged Larger than Longitudinal Stimulus. The black vertical line indicates the ratio value that provides an equal Judgment of the applied distances.

Note that Proportion Across Stimulus Judged Larger is 0.5 if a ratio Across/Along equal to 0.729 is provided. This ratio is visualized in the figure thanks to the black vertical line and it is known as Point of Subjective Equality (PSE).

However, I am going to report a better explanation about this experiment in Chapter 3.

So, the perceived distance might be a function of physical distance. That is, relationship between physical and perceive distance is not a constant.

What I have just maintained is the main subject of some experiments conducted by Barry G. Green of the Princeton University of New Jersey. The paper he wrote, called "*The perception of distance and location for dual tactile pressures*" is a clear demonstration.

In each experiment, the perceived distance was investigated by changing orientation of stimuli but also considering different body parts.

Stimuli spaced from each other at several distances were applied over different skin regions of the subjects.

Each subject responded with a number that reflected the perceived distance between the two stimuli.

Thanks to this judgment a linear relationship between perceived and physical distance has been found [***ref. 4***].

The picture below shows the comparison between two different limbs.

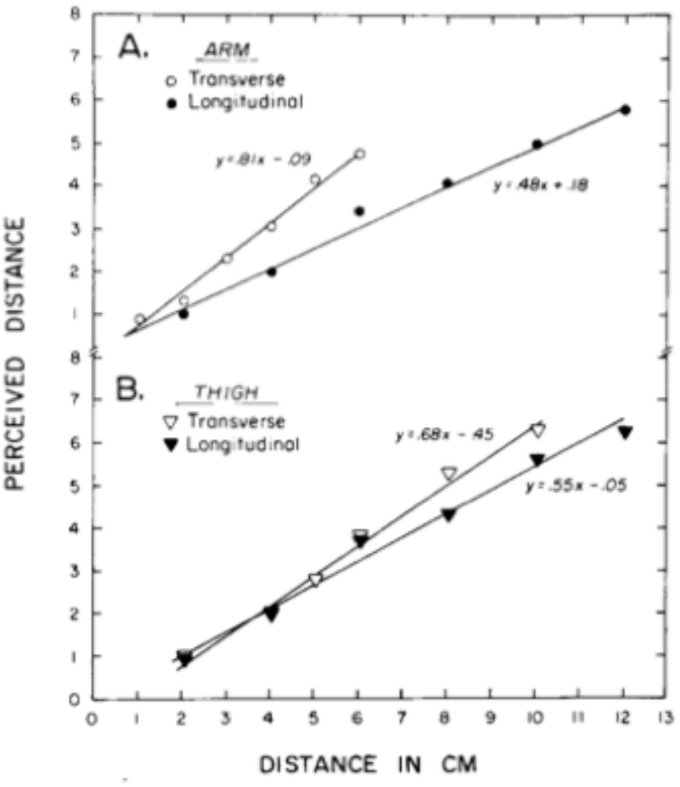


Figure 7. Perceived distance depends on both the body locus and the orientation of the stimulation.

The two limbs appear anisotropic, with, the arm showing greater anisotropy than the thigh.

So, from data reported on Green Paper, I can conclude that perceived tactile distance depends on both the body locus and the orientation of stimulation, and that the size of the orientation effect depends upon the locus. That is, the size of the orientation effect will change if the stimulated skin surface changes.

Now, the key question is: Why perceived distance differ at any body part or by changing the orientation?

As I wrote before, our brain has got an original model of our body. Considering the Primary Sensory Cortex, each part is dedicated to a specific body region. Inputs coming from the hand are elaborated within areas that differ from those areas in which inputs coming from the arm are elaborated. Moreover, each area has different dimensions. Taking a look at the sensory homunculus, it is easy to see that hands are much larger cortical representation than the arms. This is because brain provides larger area for the integration of inputs coming to the hands rather than for those coming from the arms.

Differences in term of magnification have been study by Mriganka Sur, Michael M. Merzenich and Jon H. Kaas of the Department of Psychology and Anatomy of Vanderbit University in Nashville, California.

In the paper *"Magnification, Receptive Field Area, and Hypercolumn Size in Areas 3b and 1 of Somatosensory Cortex in owl Monkeys"* they reported the magnification intensity of several owl Monkeys' body parts.

An interesting result was found. In fact, the glabrous hand or foot representations occupy nearly 100 times more cortical tissue per unit body-surface area than the trunk or upper arm representations in both areas 3b and 1 [***ref. 5***].

Figure 8 reports magnification magnitude by considering different body part. Magnification is one of several factors that can explain why there are differences in terms of perceived distance from body region to body region.

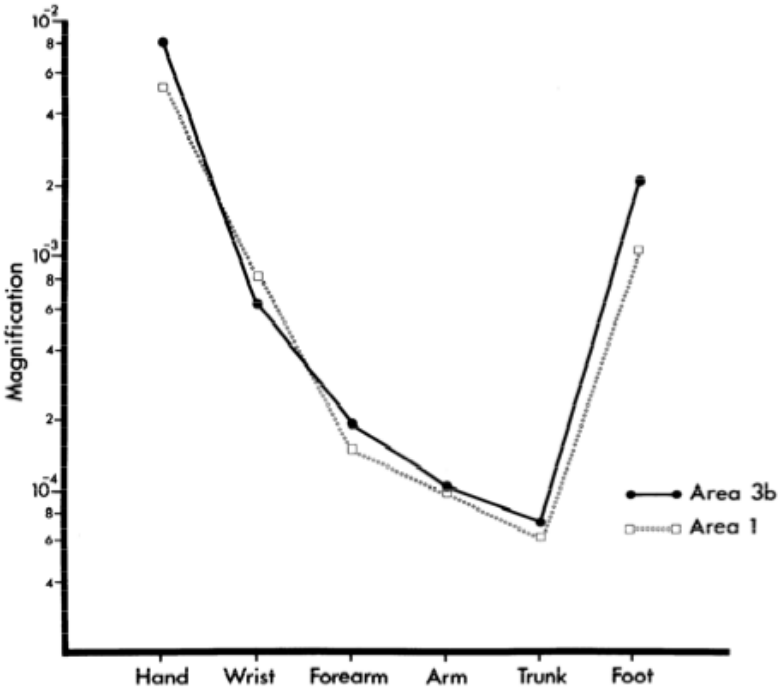


Figure 8. Difference in the perceived distance from a region to another is attributable to a different cortical magnification.

The cortical magnification is obtained by dividing the cortical representational area devoted to a body region by its skin-surface area.

In formula:

$$\mathbf{M = Cra/Ss \rightarrow Cra = M \times Ss} \qquad (1)$$

where M shorts for cortical Magnification, Cra is the Cortical Representational Area and Ss short for Skin Surface.

As a ratio of square areas, unit square measure is not necessary to describe Magnification.

So, if we consider a square area on the hand equals to 25 cm^2 (5 cm x 5 cm) and a square area over the arm equals to 100 cm^2 (10 cm x 10 cm) the cortical representational area of each body part will be different. In fact, by looking at the figure above the Magnification devoted to the hand is $\mathbf{10^{-2}}$ whereas Magnification on the arm is equal to $\mathbf{10^{-4}}$.

In particular:

Cra_Hand = 0,01 x 25 cm^2 = 0,25 cm^2

Cra_Arm = 0,0001 x 100 cm^2 = 0,01 cm^2

Cra_Hand/Cra_Arm = 0,25 cm^2 / 0,01 cm^2 = 25

So, the cortical representational area of a smaller skin region on the hand is much bigger than the cortical representational area devoted to a bigger skin surface on the arm. In this example Cra_Hand is 25 times Cra_Arm. *Difference in the perceived distance from a region to another is attributable to a different cortical magnification.*

Even if data in Figure 8 are obtained by studying brain of owl Monkeys is legitimate to think that similar data can be obtained by studying human brain. This is because somatosensory cortex of Monkeys is similar to somatosensory cortex of humans.

As stated below, different magnification factors correspond to different amounts of peripheral innervation of the represented body part, with skin surface more densely innervated having higher magnification factor. Different magnification factor correspond to different dimension of neuron RF. In particular, cortical areas with great magnification factor contain cells with smaller RFs (that is, a large number of cells is necessary to represent the surface area); cortical areas having low magnification factor have cells with larger RFs (a small number of neurons is necessary to represent the surface area).

It is known that a population of neurons in the cortex will be activating if a stimulus touches the skin surface over the RF of the population. Therefore if the RF area is large, neuronal population will represent a great skin area. Even if neurons are not activated at the same intensity, two stimuli applied over the same RF could be close enough to be undistinguished from each other by the brain. Conversely, considering smaller RF, the two stimuli could be sitting over two different RF providing the activation of two different neuronal populations. In this way stimuli can be distinguished because of a better spatial resolution.

As I have written in "*Mechanoreceptors and Receptive Fields in the skin*" there are tiny RFs in the skin of the fingertips. RF gets larger from fingers to the rest of the limb. So spatial resolution operated by the brain gets worst from the hand to the arm.

I think changing dimension of RF from body part to body part and differences in Magnification for each region of our body can explain the "classical" Weber's Illusion.

Here, I have supposed RFs with circular shape but what happen if RFs have got a shape that differ from the circular one?

The answer to this question can introduce another aspect of the Weber's Illusion. In fact, by considering a sort of anisotropy in RF's shape it is clear that tactile illusion should be detected simply by changing the orientation of the stimuli applied on the skin. Try to think at RFs with oval shape. In this way stimuli sitting along the same direction of the long axis of a RF, could fall within the same RF activating a specific neuronal population. So, stimuli could not be discriminated if they are close to each other (as the example gave before in which RF dimension changes). On the other hand, stimuli applied along the same direction of the short axis of the RFs could fall over regions represented by two different RFs. Two different populations will be activated and the two stimuli could be better distinguished. Although distance between stimuli is the same, it is not judged as equal. In other words, perceived distance changes by considering different orientation.

Moreover, a distort representation of the body inside the brain can increase anisotropy in perceived size of tactile objects and perceive distance as well. For example, if the hand is represented as being longer and more slender than it really is, distances oriented proximo-distally, along the body surface, should feel larger than those oriented medio-laterally, across the body surface. Conversely, if the hand is represented as being wider than it actually is, distances oriented across the hand should be perceived as larger than those oriented along the hand.

Longo and Haggard investigated the perceived size of tactile distances in different orientations on a single skin surface (dorsum and palm of the hand).

Several studies have found RFs representing hairy skin at many levels of the nervous system are generally oval-shaped, with the long axis running proximo-distally. Anyway, it is impossible to estimate exactly how large could be an area representing a RF. There are no studies that find out this information.

Anyway, data obtained by Longo and Haggard show that tactile stimuli running medio-laterally are systematically perceived as larger than stimuli running proximo-distally. *This suggests the body model mediating touch present a dorsum that is stretch along medio-lateral axis. Hand is represented as being wider than it actually is. This would produce the orientation-dependent tactile illusion.*

Thus, RF geometry may play a fundamental role in the construction of the implicit body model mediating tactile size and shape perception.

The figure below gives an illustrative explanation of what I have just declared.

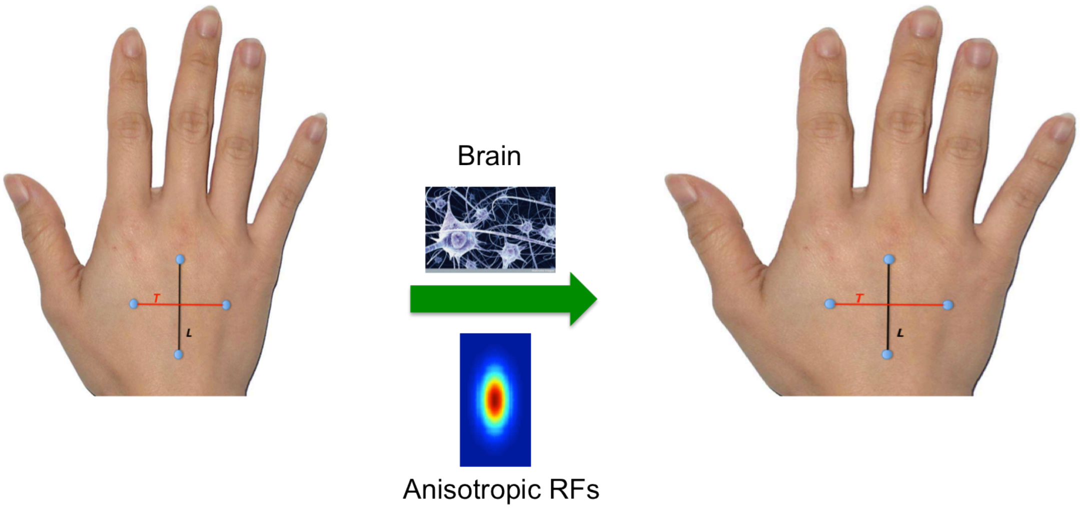


Figure 9. Orientation-Dependent Tactile illusion. Note that the red line became longer than the black one.

I focused on this relevant aspect in order to implement my model.

In addition, the experiment made by Green, shows other interesting results. For example, a physical distance equal to 4 cm, it is not judged as the same by considering different body parts.

In fact:

Physical Distance (cm)	**→**	**Perceive Distance (points)**
4 cm (Arm)	→	*2 points*
4 cm (Hand)	→	*3 points*

Data I have reported are referred to the longitudinal orientation.

Difference in terms of Perceived distance is just only one point.

It is known that somatosensory area devoted to the hand is much larger than the cortical area devoted to the arm (the ratio between them is closely to 100). *So, it seems, there is not a proportional relationship between Magnification and perceived distance. In fact, a difference higher than one point should be expected by considering what Mriganka Sur et al. have reported.*

This result suggests that an integration of inputs elaborated by primary somatosensory cortex, may exist somewhere in the brain in order to reduce the Magnification effects.

I made a similar hypothesis for the orientation-dependent tactile illusion.

Indeed, differences in term of perceived distance between transversal and longitudinal directions are not as significant as expected. In fact, some studies suggest that the long axis of RFs on the hairy skin of the limbs may be more than twice as long as the short axis [Brown et al 1975]. By considering only the shape of the RFs, tactile distance along the transversal orientation should be perceived at least twofold bigger than along the longitudinal orientation. But this is not the case. That is, *the illusion is substantially smaller than would be expected on the basis of sensitivity, cortical magnification or RF geometry*. Hence, we can hypothesize that some processes in the brain correct for the distortions characteristic of the somatosensory homunculus and RF shape, although the compensations is only partial.

This behaviour of the brain is called *rescaling*. As the brain is not able to reproduce perfect rescaling, the final result is the Weber's illusion. *Shortly, rescaling decreases Magnification effects*.

Unfortunately there are not studies that show how the brain works in order to reproduce rescaling. For that reason, this study tries to clarify this aspect via a neural network modelling study: in particular the model I implemented reproduces the orientation-dependent tactile illusion on the dorsum of the hand both inspiring by Longo and Haggard data and considering simplifying assumptions.

The main hypothesis included in this work is that there are two levels of processing of tactile inputs. The first level (lower level) may correspond to elaboration in the primary somatosensory cortex; we assume that at this lower level, codification of distance between two stimuli is strongly affected by differences in RFs size or shape (for example, at this level the same physical distance may be codified as much larger along the transversal dimension rather than along the longitudinal dimension). The second level of tactile information processing may correspond to higher somatosensory cortices. In this second level, differences in distance codification with orientation are partially rescaled; we assumed that rescaling might emerge as a network property arising from specific patterns of synaptic connections from the lower to the higher levels and inside the higher level.

In the subsequent chapters, the model will be described in details and hypotheses included in the model will be highlighted.

Chapter 2

Computational Model

Qualitative Description of the Model

As I wrote in Chapter 1 the model represents a simplification of how the brain elaborates tactile inputs sensed by skin receptors in order to obtain perceived distance between two stimuli. This is mainly a conceptual model rather than an accurate reproduction of physiological structures. So I focused on an abstract level of implementation, without specifying an exact correspondence between layers in the model and anatomical brain regions. Anyway, the mechanisms included in the model are biologically plausible.

I focused on the dorsum of the hand to study orientation-dependent tactile illusion.

I suppose that two different cortical areas integrate tactile information. One of them represents a lower-level layer (called Area1) in which a first and distorted body model is created. The other one (called Area2) works with the aim to reproduce rescaling. In other words, this is a higher-level layer that reduces the distortion of the lower level by rescaling tactile information toward their true size. Neurons in Area1 receive information from the external space (skin) and send information to neurons in Area2 via feed-forward connections.

The computational model is divided into two main parts:

- *First Elaboration Step of the External Stimuli.*

  The first layer and RFs of each neuron within Area1 represent this part.

- *Second Elaboration Step of External Stimuli.*
  Neurons within Area2 and feed-forward connections from neurons in Area1 represent this part.

First of all, tactile inputs stimulate a specific skin region of the dorsum of the hand. They have been mimicked with a Gaussian spatial pattern with a tiny deviation standard in order to reproduce stimuli very similar to punctual inputs.

The first layer in the cortex, which consists of 41x26 units, maps a skin surface area of 10 cm (longitudinal dimension) x 5 cm (transversal dimension).

Each neuron in this layer has a Receptive Field covering a specific portion of the skin region. Supposing that a topological organization exists, proximal units in the layer will respond to stimuli coming from proximal positions over the skin.

Taking a look at the matrix (41 units x 26 units) representing the lower-level layer it easy to say that centres of RFs are arranged at two different distances considering transversal (medio-lateral) and longitudinal (proximo-distal) orientation.

In fact, 26 units represent 5 cm along transversal direction whereas 10 cm correspond to 41 units along longitudinal direction. Hence, RFs centres are disposed at a distance of 0.2 cm along the transversal dimension and at a distance of 0.25 cm along the longitudinal dimension.

In formula:

5 cm / 25 units = 0.2 cm/units

(the first unit is centred in -2.5 cm and the last unit in 2.5 cm)

10 cm / 40 units = 0.25 cm/units

(the first unit is centred in -5 cm and the last unit is centred in 5 cm)

According to physiological and behavioural literature (see Chapter 1) there is a greater precision in two points discrimination along medio-lateral direction rather than proximo-distal direction. To reproduce this aspect, besides considering a different spatial resolution of RFs along the two dimensions (see below), the model considers different dimension and shape of RFs.

In fact, as I wrote in chapter 1, the smaller is the receptive field the better is the discrimination of two tactile stimuli on the skin. Anyway, not only the dimension plays an important role but also the shape of RFs.

According to data finding in literature [***ref. 5, ref. 6***] the model adopts oval-shape RFs with the long axis along proximo-distal direction. So, considering transversal orientation, RFs are much many and much smaller than on the other orientation. Thanks to these differences, the model reproduces a greater sensory acuity along the transversal dimension. As a consequence, a higher magnification of the dorsum of the hand along this direction is provided.

Like the inputs, RFs are represented by a Gaussian function with standard deviation that differs for the two orientations. In particular, (as justified later) longitudinal standard deviation is two times the transversal one.

Moreover, RFs overlap each other thanks to their dimensions and shape. In this way, a stimulus applied in a certain position on the skin region will active more neurons, specifically all neurons having RF covering that position on the skin. So, a bubble of activation in the first layer occurs.

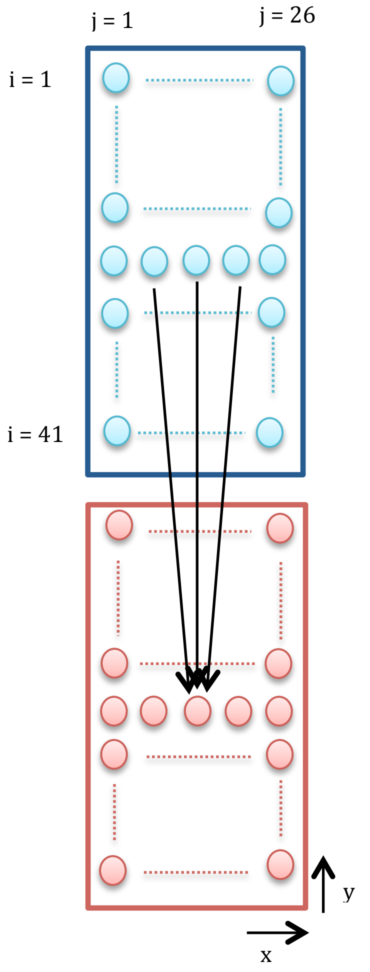
The first area improves a rough version of the perceived distance.

This is why also a second layer has been implemented as involved in tactile distance perception. It receives inputs coming from Area1.

As the first layer, a matrix of 41 rows and 26 columns represents Area2.

Feed-forward synapses connect the two layers. So, activation of each unit within the higher-level area, in response to an external stimulus, depends on the pattern of the synaptic connection from the first layer.

The figure below shows a schematic view of the model structure



First layer: 41x26 units (corresponding to 10 cm x 5 cm respectively).

Units in the first layer send synaptic connections to each unit in the second layer.

Second layer

I hypothesize that the second layer may represent higher cortical areas that - starting from a distorted primary representation based on receptor density and cortical magnification - may partially rescale tactile information towards their true size.

The model not only implements feed-forward synapses, but also lateral synapses (not reported in the figure above).

Feed-forward synapses ensure communication from Area1 to Area2.

Lateral synapses improve communication between each unit at any layer. In particular, these synapses are arranged according to a Mexican hat disposition, i.e. excitatory synapses among proximal neurons and inhibitory ones among distal neurons. This arrangement of lateral synapses improves two points discrimination.

Qualitative description of model working

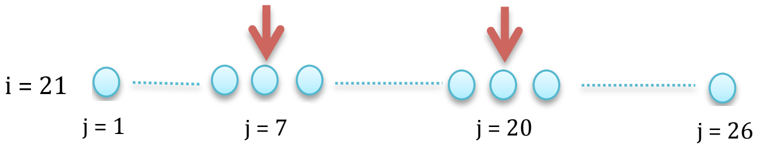
In this section, I will describe how the model works qualitatively. In particular, I will present the pattern of neuron activation that it is expected to obtain in the two layers of the model.

Response of lower-level area to two points stimulation

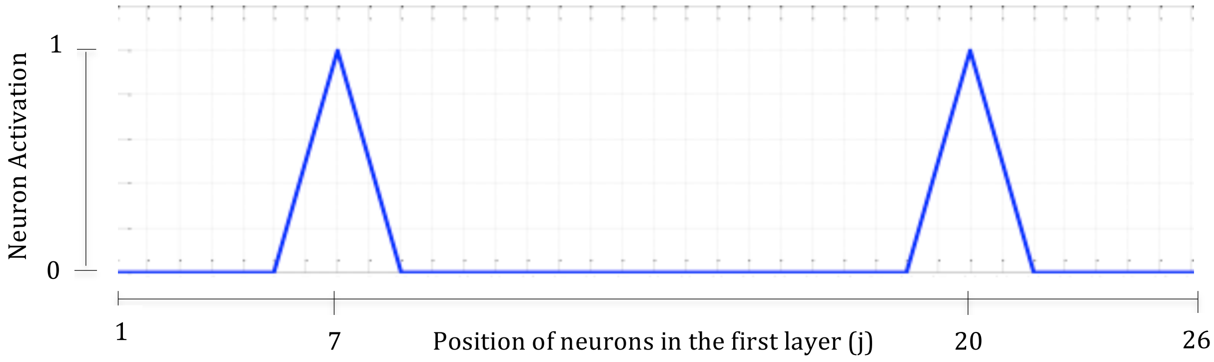
Suppose that a tactile stimulation consists of two punctual stimuli at about 2.5 cm distance is applied.

For example, assume we stimulate units in the central row of the matrix. Below, a graphical representation is reported.

Transversal Direction:



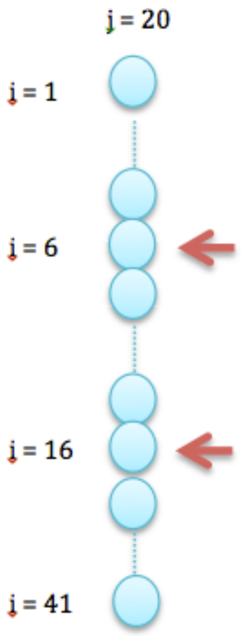
The red arrows represent the external punctual stimuli applied at two skin positions. Let's assume that the position of one stimulus corresponds to the RF centre of the neuron of the first layer at position j = 7 (RF centre = j*0.20 cm = 1.4 cm) and the position of the second stimulus corresponds to the RF centre of the neuron of the first layer at position j = 20 (RF centre = j*0.20 cm = 4 cm). The expected activation of the neurons in the row (first layer) is something like this:



In order to solve perceived distance I considered the number of neurons between the two peaks of activation. In this example a perceived distance equal to 13 neurons is reported.

A similar discussion can be made with regard to punctual stimuli applied along the longitudinal orientation.

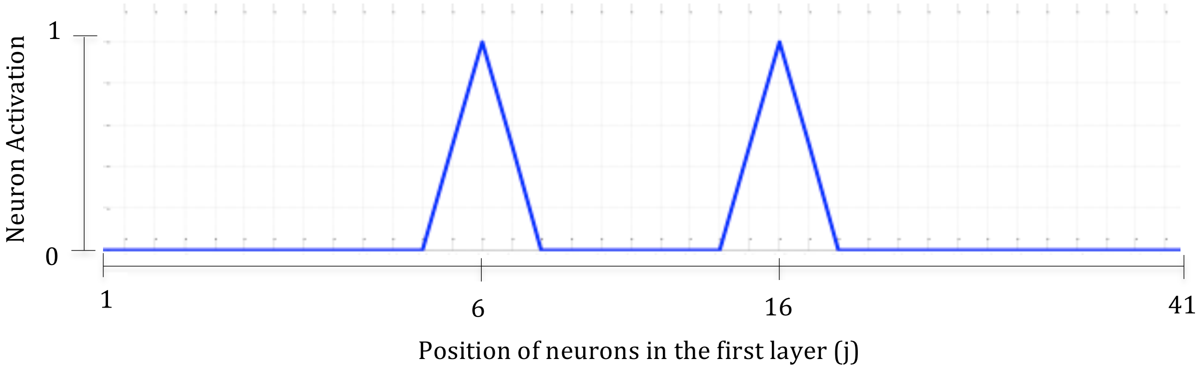
Longitudinal Direction:



Here, each neuron is design bigger just to remember that along this orientation there is less resolution.

The red arrows represent the external punctual stimuli applied in two skin positions corresponding respectively to the RF centre of the neuron of the first layer at position i = 6 (RF centre = i*0.25 cm = 1.5 cm) and to the RF centre of the neuron of the first layer at position i = 16 (RF centre = j*0.25 cm = 4 cm).

The expected activation of the neurons in the row (first layer) is something like this:



Here, the perceived distance (by adopting the same metric as above, that is the number of neurons between the two peaks of activation) is equal to 10.

Now, we can think about the first layer implemented by the model as that area in the primary somatosensory cortex devoted to the hand. Taking a look at the distance codified by this layer (remember that the applied distance is the same along the two orientations = 2.5 cm), a ratio (Transversal/Longitudinal) higher than one is found.

Transversal = 13;
Longitudinal = 10;
Ratio = 13/10 = **1.3**;

This result may be interpreted in this way: the same distance between two punctual stimuli applied externally is perceived bigger when the stimulation is applied along the transversal orientation rather than along the longitudinal orientation.

Response of higher-level area to two points stimulation

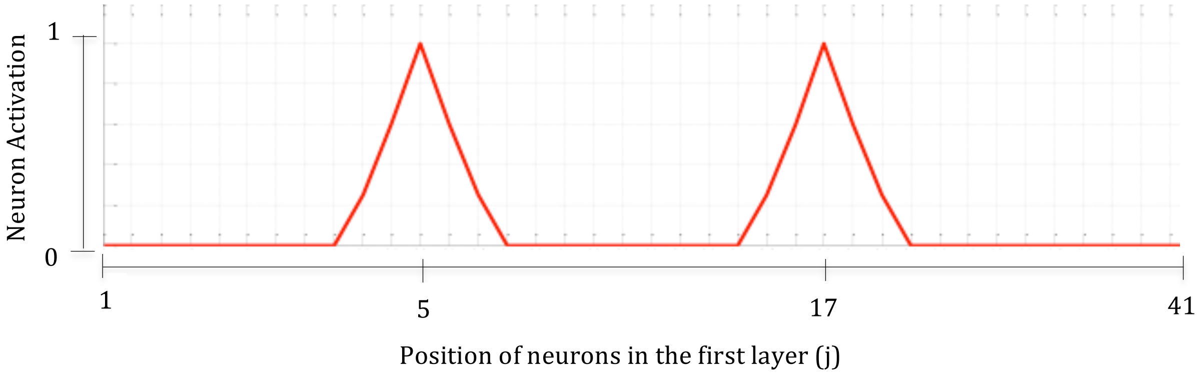
Area2 provides an improvement of the body model obtained within Area1. That is, *Area2 acts in order to reduce the discrepancy between the two distances as reported by Area 1.*
So, I assume that the final output of the neuronal network is the activation observed in Area2. This means, activation in Area2 is read out in order to produce the response of our hypothetical subject. We assume that the distances perceived by our hypothetical subject correspond to the number of neurons between the two peaks of activation in Area2.
As I wrote in Chapter 1 it is unknown how the brain rescales tactile inputs coming from lower-level layer. Several hypotheses have been made. A plausible hypothesis is that the brain has learned (by integrating various sensory information such as visual, tactile, proprioceptive information) to rescale tactile information from skin regions having different cortical extents. In this case, the Weber's Illusion would reflect a failure to perform a complete rescale.
I assume that this brain capability is implemented through the synaptic connections from the first layer to the second layer (and that

these synapses would have been learned via training and experience). Area1 sends feed-forward synapses that work in order to preserve perceived distance along transversal direction changing the one along the longitudinal orientation. It means that distance in terms of number of neurons has same value in both lower-level area and higher-level area if a transversal stimulation is considered, whereas it is not the same along longitudinal direction. In particular, perceived distance along transversal direction is preserved while perceived distance along longitudinal direction increases within Area2.

I adopted this solution in order to change perceived distance value along the orientation with less spatial resolution and less sensory acuity. In fact, it is licit to think that nothing should change from Area1 to Area2 (in term of perceived distance) if transversal stimuli are applied because of both better spatial resolution and sensory acuity. Here a better judgment of distance is provided. In other words, it seems ecologically more beneficial to improve the functionality where it is poorer (that is along the orientation showing lower resolution) and to preserve it where it is higher (that is along the orientation showing better resolution).

So, an activation in Area2 due to a longitudinal stimulation have to enlarge the gap between the two peaks, that is, the number of neurons between them must become higher.

Hence, the output, relative to the example made before for Area2 should be something like this:



So, longitudinal perceived distance is equal to 12 neurons in Area2.

The situation is a bit different comparing these results to those ones in Area1.
In fact:

Transversal = 13;
Longitudinal = 12;
Ratio = 13/12 = **1.08**;

The ratio in Area2 is closer to one than in Area1.
It is important that the ratio should not be equal to one, if so, dependent-orientation tactile illusion would not be replicated.

Mathematical Description

In the following, I will report a mathematical description of the neuronal network.
I will show mathematical formulas that represent each important part of the model. Values of each symbol, which appear in each formula, will be reported in *Table 1*.
The superscripts *f*, *s* will denote the first and the second layer respectively whether the superscripts *T* and *L* will denote the transversal and longitudinal direction.
First of all, it is important to say that both lower-level layer and higher-level layer are represented by NxM neurons (N=41 (y direction), M=26 (x direction)). Each unit of rectangular matrix representing Area1 integrates inputs coming from the skin surface of the dorsum of the hand. Units of rectangular matrix, which represent Area2, integrate inputs coming from Area1.
Each neuron in the first layer has a specific RF on the skin. RFs of neurons are arranged at a distance of 0.2 cm, one from each other, along the x direction (transversal direction), while along the y direction (longitudinal direction) they are arranged at a distance of 0.25 cm one from each other.
By considering y_i and x_i as the coordinates that identify the centre of

the RF of a generic neuron ij, I can write:

$$\begin{aligned} \mathrm{y_i} &= -5.25\,cm + i \cdot 0.25\,cm \quad (i = 1,2,\dots,N1) \\ \mathrm{x_i} &= -2.7\,cm + j \cdot 0.2\,cm \quad (i = 1,2,\dots,M1) \end{aligned} \tag{2.1}$$

By assuming this convention, the centre of the frame of reference is set at the centre of the represented skin surface (i.e. the spatial coordinates x and y span respectively from -2.5 cm to +2.5 cm and from -5 cm to +5 cm)

Receptive Fields

Hereinafter, the RF will be denoted with the symbol Φ. Each RF is described with a Gaussian function. Hence, each RF is descripted by the equation below:

$$\Phi_{ij}^{f}(\mathrm{x,y}) = \Phi_0^f \cdot exp\left(-\left(\frac{\left(x_i^f - x\right)^2}{2\cdot\left(\sigma_x^\Phi\right)^2} + \frac{\left(y_j^f - y)^2\right)}{2\cdot\left(\sigma_y^\Phi\right)^2}\right)\right) \tag{2.2}$$

where $\sigma_y^\Phi > \sigma_x^\Phi$.

In *equation 2.2*, x_i^f and y_j^f indicate the centre of the RF, x and y are the spatial coordinates, Φ_0^f represent the strength of the Gaussian function and σ_x^Φ and σ_y^Φ are the standard deviations of the Gaussian function along medio-lateral and proximo-distal orientation respectively (three standard deviations approximately cover the overall RF).

I opted for two different standard deviations (one for both directions) in order to reproduce RFs with oval-shape. Indeed, physiological data [*Ref. 3*] suggest that RFs in the skin region of the dorsum of the hand have an anisotropic shape

However, it is unknown which is the correct dimension of RFs in the hand of humans. Anyway, by considering several experiments made on cats and monkeys [*Ref. 5; Ref. 6*] we know RFs in their limbs are greater along proximo-distal axis than medio-lateral one. In particular, it seems the long axis of RF is about twice or triple the short axis. That is why in the model σ_y^Φ value is twice the σ_x^Φ value. Moreover thanks to both different standard deviations and different spatial resolution, RFs are overlapping one from each other. An important thing to say is that the per cent of overlapping is the same in each direction. In fact, setting a ratio between the standard deviations equal to the ratio between longitudinal and transversal dimensions of the dorsum this result is provided.

Figure 1 shows the RF of the neuron located in the centre of Area1 (position 21,13).

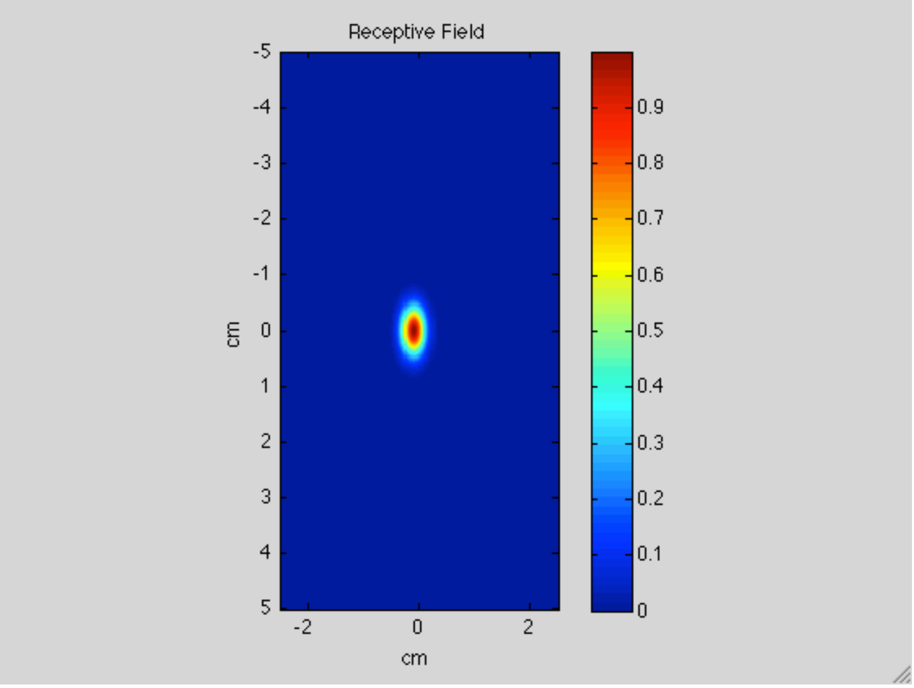


Figure 1. Receptive Field of a neuron in the lower level area.

A colour bar is used to indicate the strength of the RF (that is the contribution given by the RF to the received input). So, if a stimulus is applied over the centre of that RF, the magnitude of the input due to the external stimulus will be equal to the intensity of the stimulus (on that point on the skin). In fact, setting $x = x_i^f$ and $y = y_i^f$, $\Phi_{ij}^f(\mathrm{x,y})$ will be equal to Φ_0^f (whose value is assumed equal to one).

Conversely, if the stimulus will apply distant from x_i^f and y_i^f the contribution will be lower or null.

According to *equation 2.2*, an external stimulus applied at the position x, y excites not only the neuron centred in that point but also the proximal neurons with RFs covering that position.

External Input

The model simulates external inputs by a two-dimensional Gaussian function. I used a very small standard deviation in order to reproduce punctual stimulus with circular shape.

In formula:

$$I^{f,T}(x,y,t) = \begin{cases} 0, & t < t_0 \\ I_0^{f,T} \cdot \exp\left(-\frac{\left(x_0^{f,T}-x\right)^2+\left(y_0^{f,T}-y\right)^2}{2\cdot\left(\sigma_I^{f,T}\right)^2}\right), & t \geq t_0 \end{cases} \qquad \textbf{(2.3)}$$

where t$_0$ is the instant of stimulus application, $x_0^{f,T}$, $y_0^{f,T}$ is the central point of the stimulus, and $I_0^{f,T}$ and $\sigma_I^{f,T}$ represent the amplitude and the standard deviation.

Therefore, two different stimuli are provide in order to compute the perceived distance between them. Hence, the total input correspond to the sum below:

$$I^{f,T}(x,y,t) =$$
$$\begin{cases} 0, & t < t_0 \\ I_1^{f,T} \cdot \exp\left(-\frac{\left(x_1^{f,T}-x\right)^2+\left(y_1^{f,T}-y\right)^2}{2\cdot\left(\sigma_I^{f,T}\right)^2}\right) + I_2^{f,T} \cdot \exp\left(-\frac{\left(x_2^{f,T}-x\right)^2+\left(y_2^{f,T}-y\right)^2}{2\cdot\left(\sigma_I^{f,T}\right)^2}\right), & t \geq t_0 \end{cases} \qquad \textbf{(2.4)}$$

where $x_1^{f,T}$, $y_1^{f,T}$ is the central point of one stimulus and $x_2^{f,T}$, $y_2^{f,T}$ is the central point of the other stimulus.

These formulas are referred to the transversal orientation (see T as the apex in I). Anyway, the same formulas are provided for the longitudinal orientation. In fact, it is possible to change the two-point stimulation orientation by changing x_1, y_1, and x_2, y_2.

The next figures (Figure 2.a, and Figure 2.b) show couple of stimuli applied along transversal and longitudinal direction respectively. Pictures regarding external stimuli, and input to neurons, and activation in both Area1 and Area2 are referred to a simulation distance equal to 3 cm.

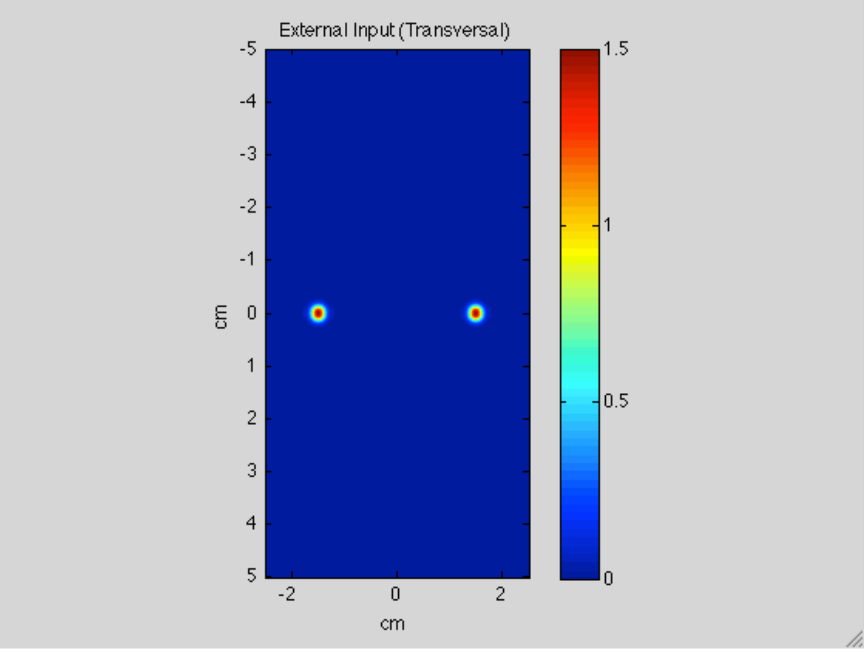


Figure 2.a. Punctual external stimuli applied across the dorsum of the hand.

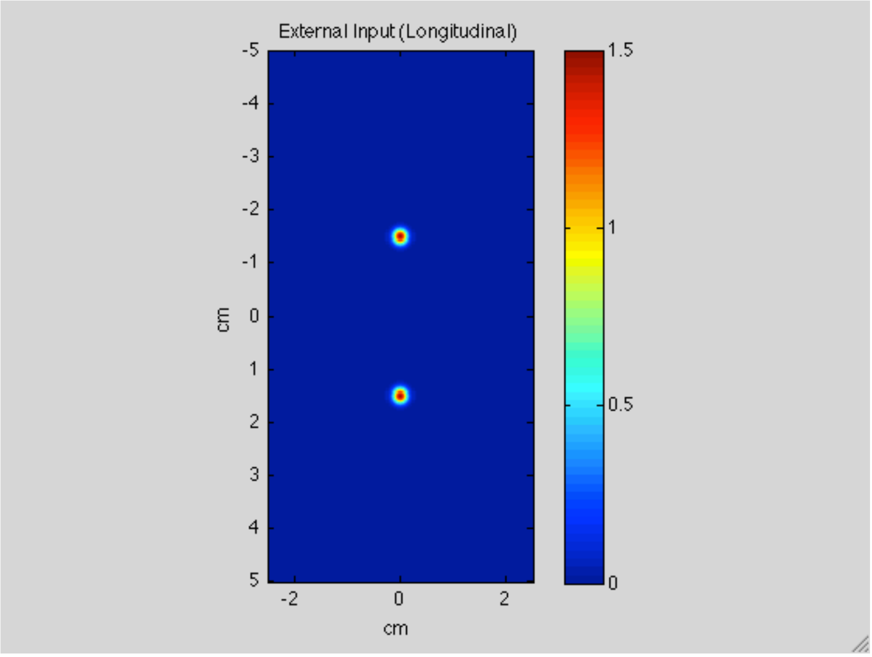


Figure 2.b. Punctual external stimuli applied along the dorsum of the hand.

Activity of the lower-level neurons

The total input received by a generic neuron *ij* in the lower-level area is the sum of two contributions:

- The contribution due to the external stimuli (say, $\varphi_{ij}(t)$, since it depends on the RF Φ_{ij}).
- The contribution due to the Lateral Synapses linking the neuron with the other elements in the same area (say, $\lambda_{ij}(t)$, lateral).

Each contribution will be described below.

The input $\varphi_{ij}^{f,T}$ that reaches the neuron *ij* in the presence of an external stimulus is computed as the inner product of the stimulus and the receptive field, according to the following equation:

$$\varphi_{ij}^{f,T}(t) = \int_x \int_y \Phi_{ij}^{f}(\mathrm{x,y}) \cdot I^{f,T}(x,y,t)dxdy \cong \sum_x \sum_y \Phi_{ij}^{f}(\mathrm{x,y}) \cdot I^{f,T}(x,y,t)\Delta x\Delta y \quad \mathbf{(2.5)}$$

where $I^{f,T}(x,y,t)$ is the tactile external stimulus applied on the dorsum of the hand at the coordinates x, y and at the time t. The right-hand member of *equation 2.5* means that the integral is computed with the histogram rule (with Δx = Δy = 0.0312 cm).

In other words, *external inputs of lower-level neurons are filtered by their respective RFs*.

Figure 3.a and 3.b show the interaction between RF and external stimulus in both Transversal and Longitudinal case (that is the final value of the input that each neuron receives as a consequence of the external stimulation).

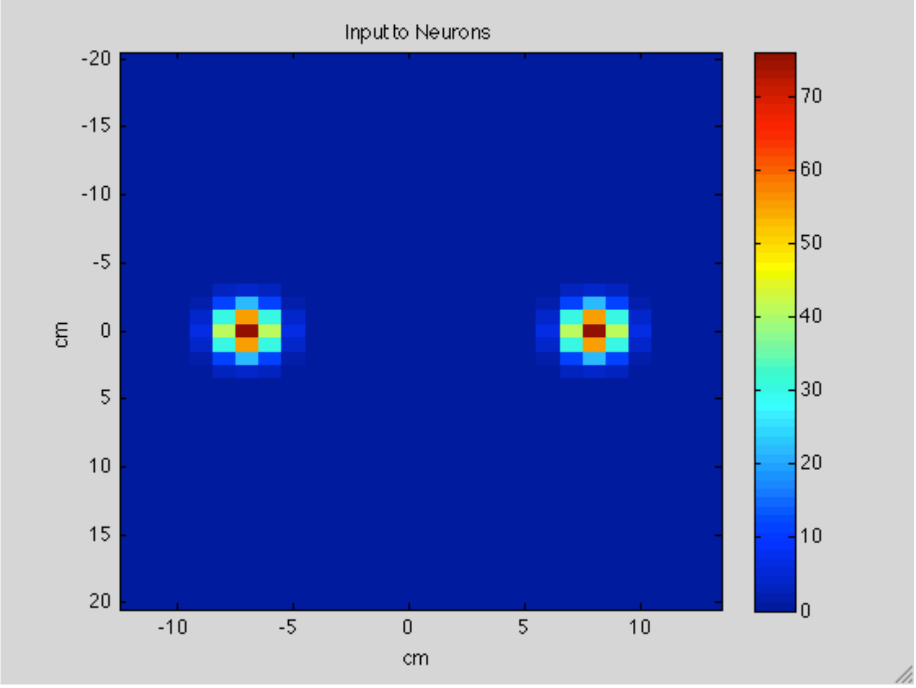


Figure 3.a. Inputs to neurons within the lower-level layer depend on the interaction between RFs and external stimuli.

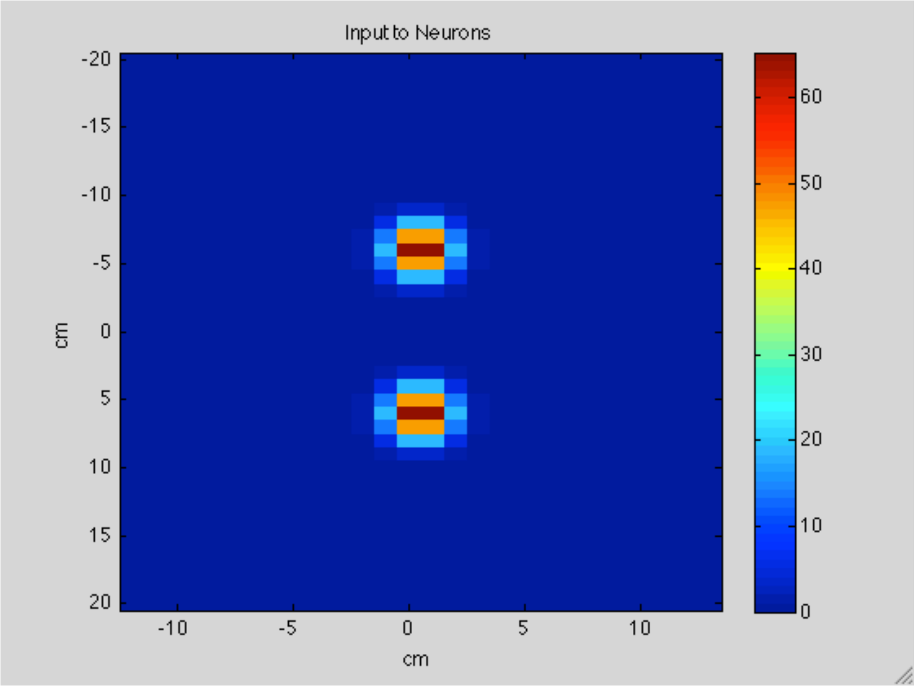


Figure 3.b. **Inputs to neurons within the lower-level layer depend on the interaction between RFs and external stimuli.**

In particular, each coloured square in the picture represents the input that each neuron in Area1 receives as a consequence of external stimulation.

Note that by setting both different spatial resolution and oval-shape of RFs, the distance between the two stimuli looks different across the two orientations. In particular, the distance between the two bubbles of activation results larger when the two stimuli are applied along the transversal orientation than along the longitudinal orientation.

Now I am going to explain the second input contribution. This is an input that a lower-level neuron receives from other neurons within the same area via lateral synapses. It is defined as

$$\lambda_{ij}^{f}(t) = \sum_{h=1}^{N} \sum_{k=1}^{M} L_{ij,hk}^{f} \cdot \chi_{hk}^{f}(t) \qquad \textbf{(2.6)}$$

$\chi_{hk}^{f}(t)$ represents the activity of the hk neuron in the Area1, which in the model is a state variable. $L_{ij,hk}^{l}$ indicates the strength of the synaptic connection from the presynaptic neuron at the position hk to the postsynaptic neuron at the position ij. These synapses are symmetrical and are arranged according to a Mexican hat function. Both Area1 and Area2 have same lateral synapses described by the equation below.

$$L_{ij,hk}^{l} = \begin{cases} L_{ex} \cdot exp\left(-\frac{\left(x_i^l - x_h^l\right)^2 + \left(y_j^l - y_k^l\right)^2}{2\cdot\left(\sigma_{ex}^l\right)^2}\right) - L_{in} \cdot exp\left(-\frac{\left(x_i^l - x_h^l\right)^2 + \left(y_j^l - y_k^l\right)^2}{2\cdot\left(\sigma_{in}^l\right)^2}\right), ij \neq hk \\ 0, \qquad ij = hk \end{cases} \qquad \mathbf{(2.7)}$$

$$\boldsymbol{l = f,\ s}$$

where x_i^l and y_i^l identify the position of the neuron ij within the layer whereas x_h^l and y_k^l identify the position of the neuron hk within the same layer.

L_{ex} , and σ_{ex}^l define the excitatory Gaussian function whether the parameters L_{in} and σ_{in}^l are referred to the inhibitory one.

In other words, the parameters above define the strength and the extension of these synapses.

Moreover, to have a Mexican hat disposition, the following condition must be satisfied:

- $L_{ex} > L_{in}$
- $\sigma_{ex}^l < \sigma_{in}^l$

Note that the null term in *equation 2.7* avoids the auto-excitation of each neuron.

Figures 4.a, and 4.b show synaptic connections between a neuron in position (0,0) (the neuron that is sitting in the centre of the rectangular matrix) and all the other neuron within the first layer. In particular, each coloured square is the synaptic weight that (0,0) neuron receives from the neuron in the correspondent position.

It is clear that connections between (0,0) neuron and neurons sitting right next to it are stronger than connections between the same unit and units sitting father apart. Moreover, further distant neurons send inhibitory synapses to (0,0) neuron.

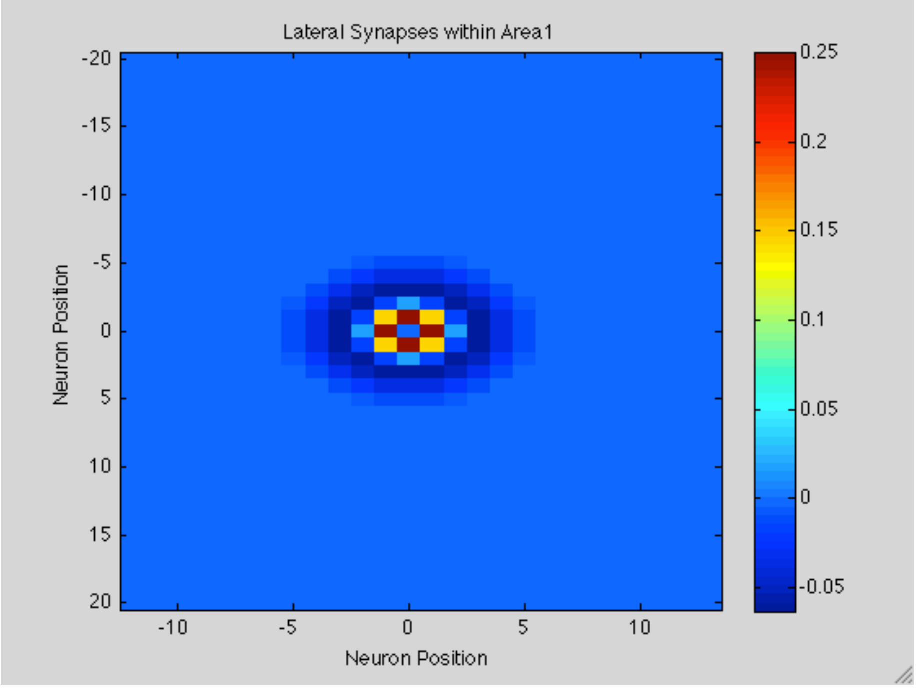


Figure 4.a. Pattern of lateral synapses of neuron in position (0,0) receives from all the other neurons within the same layer.

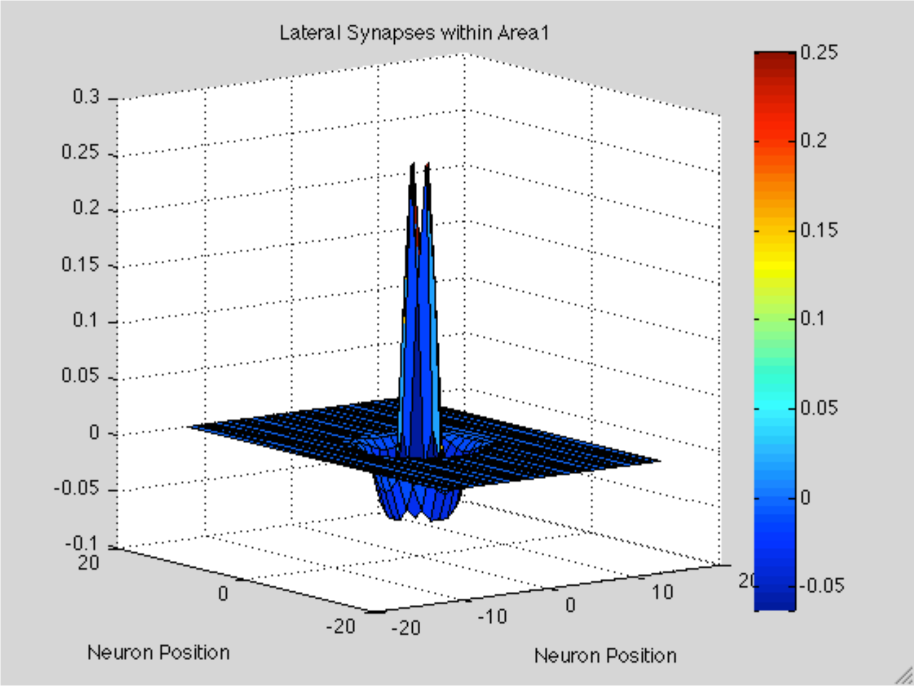


Figure 4.b. 3-D view of the Lateral synapses. The Mexican hat shape is highlighted.

Figure 4.b, gives us a 3D view of lateral synapses connection in order to highlight the Mexican hat shape they have.

Finally, the total input (say, $u_{ij}^{f}(t)$) received by neurons within the first layer is the sum of the two different contributions below.

$$u_{ij}^{f}(t) = \varphi_{ij}^{f,T}(t) + \lambda_{ij}^{f}(t) \qquad \textbf{(2.8)}$$

Then, neuron activity is computed from its input through a first-order dynamics and static sigmoidal relationship:

$$\tau \frac{d\chi_{ij}^{f}(t)}{dt} = -\chi_{ij}^{f}(t) + F(u_{ij}^{f}(t)) \qquad \textbf{(2.9)}$$

In particular:

$$F(u) = \frac{G_{max}}{1 + exp(-\gamma(u - u_0))}$$

where F(u) represents the sigmoidal function. G_{max} is the static gain of the sigmoidal and it represents the maximum activation value assumed by a generic neuron. That is, G_{max} is the upper saturation value of the sigmoid and it is set equal to 1. In this way neuron activity is normalized with respect to its maximum. u_0 is the value that the input have to assume in order to reproduce an activation equal to half G_{max} ($\frac{G_{max}}{2}$). γ is a parameter that sets the slope of the sigmoid at its central point. Of course, the higher is $u_n^{ij,f}$, the higher is the activation. The lower is $u_n^{ij,f}$, the lower is the activation.

τ is the time constant of the differential equation.

We can compute *equation 2.9* using Euler's method.

In this way:

$$\frac{d\chi_{ij}^{f}(t)}{dt} = \frac{\chi_{ij}^{f}(t+\Delta t)-\chi_{ij}^{f}(t)}{\Delta t} \tag{2.10}$$

So, I can write:

$$\chi_{ij}^{f}(t+\Delta t) = \chi_{n+1}^{ij,f}$$

$$\chi_{ij}^{f}(t) = \chi_{n}^{ij,f}$$

Note that $\chi_{n}^{ij,f}$ indicates the neuron activity at the step *n* whether $\chi_{n+1}^{ij,f}$ is the neuron activity at the following step.

Obviously, Δt is the simulation step.

By substituting the expression below in *equation 2.9* I obtain the discretization version of the same formula.

$$\chi_{n+1}^{ij,f} = \chi_{n}^{ij,f} + \frac{\Delta t}{\tau}\left[-\chi_{n}^{ij,f} + F(u_{n}^{ij,f})\right] \tag{2.11}$$

I considered a simulation runtime equal to 200 steps. Δt is the simulation step and the value that it assumes is 0.5 ms. So we can say that the simulation runtime is 100 ms.

At the end of the simulation two bubbles of activation compose the pattern in Area1. Neurons sitting in the centre of the bubbles present a higher activity than neurons on the edge of the bubbles. The range of activation spread from the null value to the unit one (0-1). The colour bar explains the range values.

Figures 5.a, and 5.b show the activation of neurons within the lower-level area if stimuli along transversal orientation are applied on the skin.

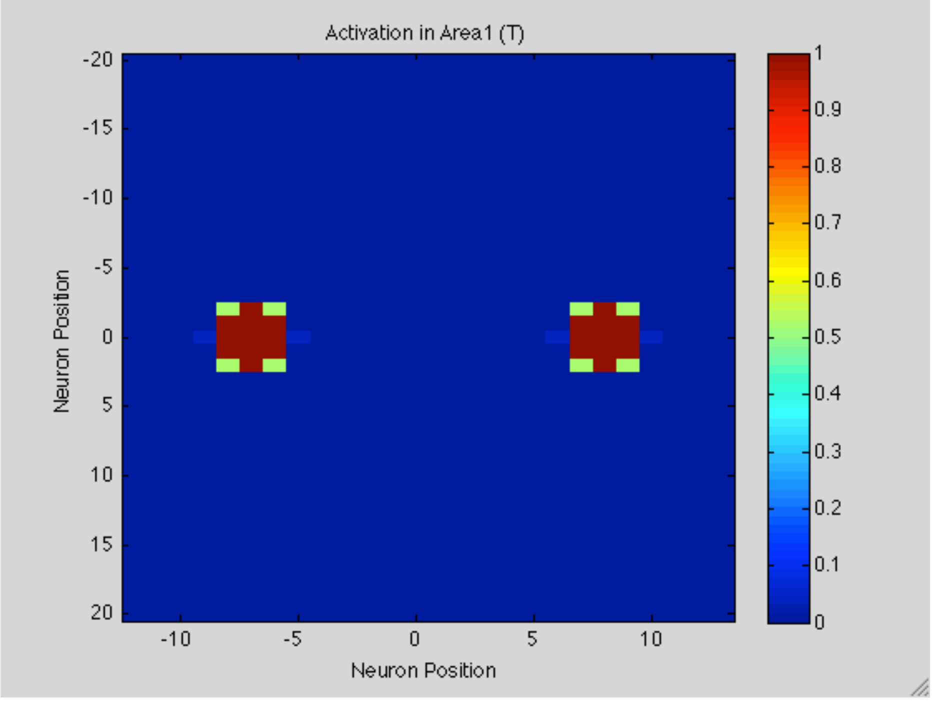


Figure 5.a. Pattern of activation within the lower-level layer by considering a stimulation across the dorsum of the hand.

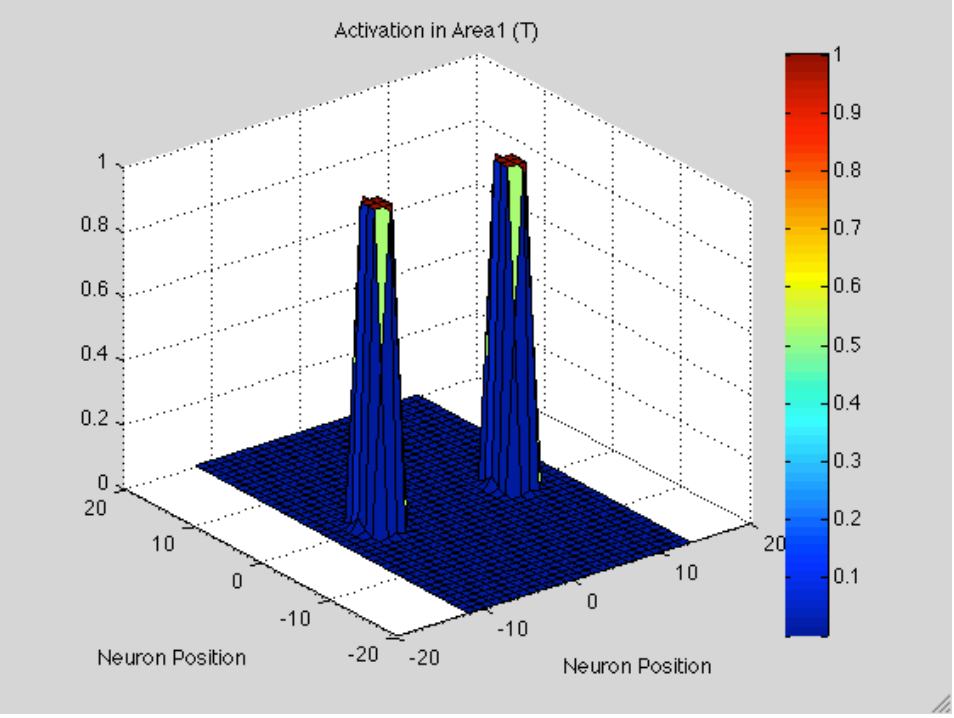


Figure 5.b. 3-D view of the activation pattern. The two peaks of activation are clearly discriminated.

Figure 5.b is a 3D version of Figure 5.a. As mentioned in the previous paragraph, I assume that the distance between the two

points of stimulation is coded in terms of neurons between the two peaks of activation. More specifically, an activation threshold has been considered. It means that neurons with a magnitude of activation upper than the threshold value are considered as maximally activated. This is why is more correct to talk about a bubble of maximally activated neurons instead of peaks of activation. So, in the model, the perceived distance is assumed as the number of neurons between the two maximal activation bubbles.

Similar declarations have been made for the longitudinal case (see the figures below).

The threshold of activation is equal to 0.9, which correspond to the 90% of the maximum activation value (G_{max}).

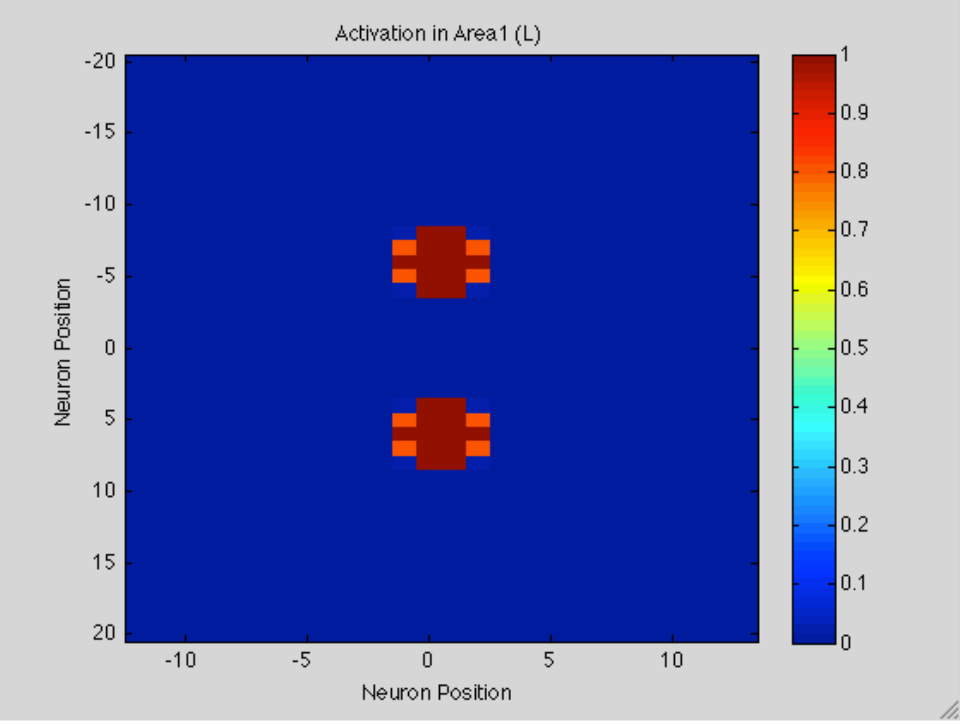


Figure 6.a. Pattern of activation within the lower-level layer by considering a stimulation along the dorsum of the hand.

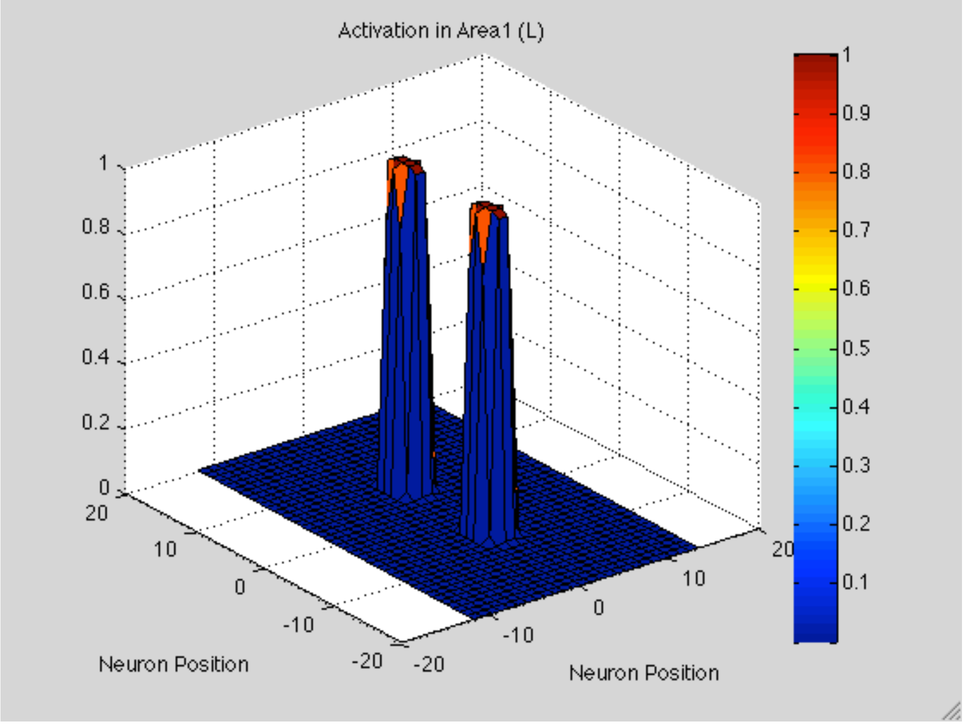


Figure 6.b. 3-D view of the activation pattern. The two peaks of activation are clearly discriminated.

The pictures clearly indicate orientation-dependent tactile illusion plays a key rule in Area1 since distance between bubbles of activation sitting in the transversal orientation strongly differs from that one along the longitudinal direction. In fact, just 8 neurons encode for the applied distance along the hand whereas the same distance, across the hand, is represented by 13 neurons.

However activation of neurons in the first layer is a part of the input that will reach neurons within the second layer through feed-forward synapses.

In the next paragraph I am going to explain how feed-forward synapses operate in order to rescale perceived distance elaborated in Area1.

Activity of the higher-level neurons

Area2 in the model represents a higher-level layer that elaborates inputs from the lower-level layer.

As in Area1, the total input received by a generic *ij* neuron is the sum of two contributions:

- The contribution due to neurons in Area1.
  Feed-forward synapses link neurons in Area1 to neurons in Area2. These synapses have a Gaussian distribution avoiding inhibitory effects. That is, feed-forward synapses produce only excitatory effects.
- The contribution due to the lateral synapses linking the neurons with the other elements in the same area (see *equation 2.6* and *equation 2.7*)

The equations corresponding to the mechanisms described above are the following.

$$u_{ij}^{s}(t) = \psi_{ij}^{s}(t) + \lambda_{ij}^{s}(t) \qquad \textbf{(2.13)}$$

where $u_{ij}^{s}(t)$ is the *ij* neuron input at a certain time instant. $\psi_{ij}^{s}(t)$ is the feed-forward synapses contribution. Note that I used the apex "*s*" in order to discriminate the second layer to the first one.
In particular:

$$\psi_{ij}^{s}(t) = \sum_{h=1}^{N} \sum_{k=1}^{M} W_{ij,hk}^{f\to s} \cdot \chi_{hk}^{f}(t) \qquad \textbf{(2.14)}$$

In *equation 2.14* the term $W_{ij,hk}^{f\to s}$ correspond to feed-forward synapses strength that *ij* neuron within Area2 reaches from *hk* neuron within Area1.
The strength of the feed-forward synapse is set by the following equation:

$$W_{ij,hk}^{f\to s} = W_{0}^{f\to s} \cdot exp\left(-\left(\frac{\left(x_i^s - x_h^f\right)^2}{2\cdot\left(\sigma_x^{\mathrm{W}}\right)^2} + \frac{\left(y_j^s - y_k^f)^2\right)}{2\cdot\left(\sigma_y^{\mathrm{W}}\right)^2}\right)\right) \qquad \textbf{(2.15)}$$

where $\sigma_x^{\mathrm{W}} > \sigma_y^{\mathrm{W}}$.

In *equation 2.15*, x_i^s, and y_i^s represent the position of *ij* neuron in Area2, whether x_h^f, and y_k^f indicates the position of *hk* neuron in Area1. σ_x^{W}, and σ_y^{W} are the standard deviations of the Gaussian functions along the medio-lateral and proximo-distal orientation. σ_x^{W} is two times σ_y^{W}. In this way, feed-forward synapses have an oval-shape with the long axis parallel with the transversal direction. An important thing to say is that the exponential term assumes a value equal to 1 when the coordinates of the two neurons presented the same value. Then the feed-forward synapses strength between them will be the highest one. In other words, the *ij* neuron receives the strongest connection from that neuron in Area1 with the same spatial position (*i*=*h*, *j*=*k*).

Thanks to this pattern of feed-forward excitation, a bubble of activation in Area1 produces in Area2 a bubble of activation, which is narrower along the longitudinal direction. In particular, values of parameters of the synapses have been set so that in case of transversal stimulation the perceived distance is the same in the two Areas, whereas in case of longitudinal stimulation, the perceived distance increases when passing from Area1 to Area2. So, a rescaling effect is present.

The following figures (Figure 7.a, and Figure 7.b) illustrate what I have just explained.

The feed-forward synapses in the picture are referred to neuron in (0,0) position within Area2. Of course, each coloured square indicate the connection strength between the neuron in Area1 at the indicated position and the neuron within Area2 at 0,0 position.

Note that, that neuron at position (0,0) in Area2 receives a maximal contribution from the neuron in the same position in Area1.

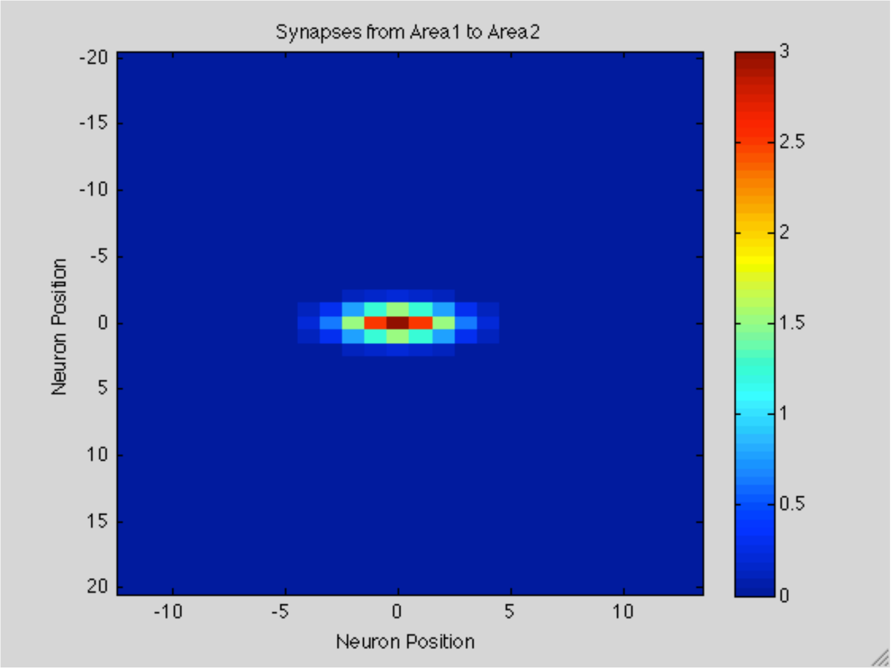


Figure 7.a. Feed-forward synapses from the first layer to the second one. The pattern is referred to the neuron in (0,0) position within the second layer. Note that it receives a maximal contribution from the neuron in the same position within the first layer.

In the next picture a 3D representation of the feed-forward synapses is shown. Note that, they provide only excitatory effects.

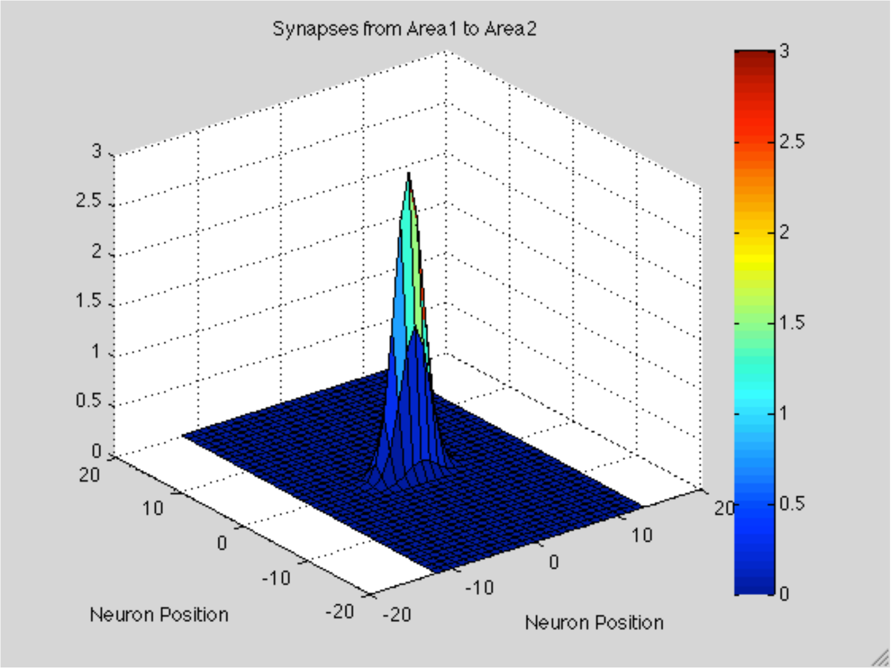


Figure 7.b. 3-D view of the Feed-forward synapses. Only excitatory effects are provided.

Anyway, also lateral synapses in the high-level area plays an important role in order to provide rescaling.
Here I will not show them because they are as lateral synapses within the first layer.
Thanks to both feed-forward and lateral synapses the bubbles of activation within Area2 have different shape and size with respect to those in Area1. While they preserve the dimension along the transversal direction, they become shrink along the longitudinal direction, increasing the gap between them. It is clear that in Area2 bubbles of activation have an oval-shape.
Actually size and shape of each bubbles of activation, not only change from layer to layer but also from transversal to longitudinal orientation. In fact, supposing to stimulate the dorsum of the hand with identical stimulation both along medio-lateral and proximo-distal direction, dimensions of bubbles of activation in Area2 strongly depend on the orientation (see Figures 8.a, 8.b, 8.c, and 8.d below).

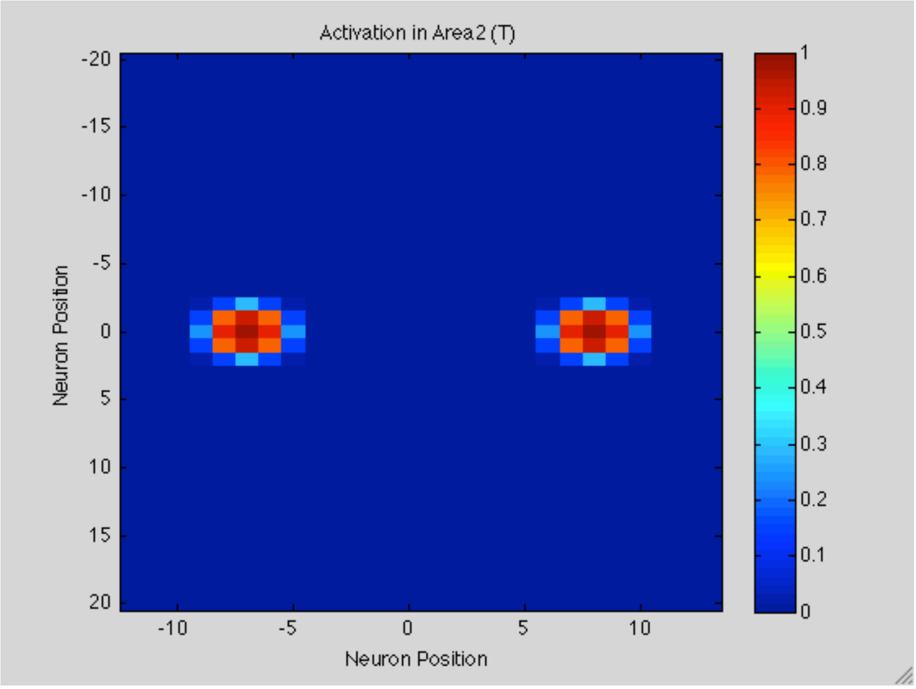


Figure 8.a. Pattern of activation within the higher-level layer if stimuli across the hand are spaced at a distance equal to 3 cm. The edges of the bubbles of activation are much more blurred than those referred to the bubbles within the lower-level layer

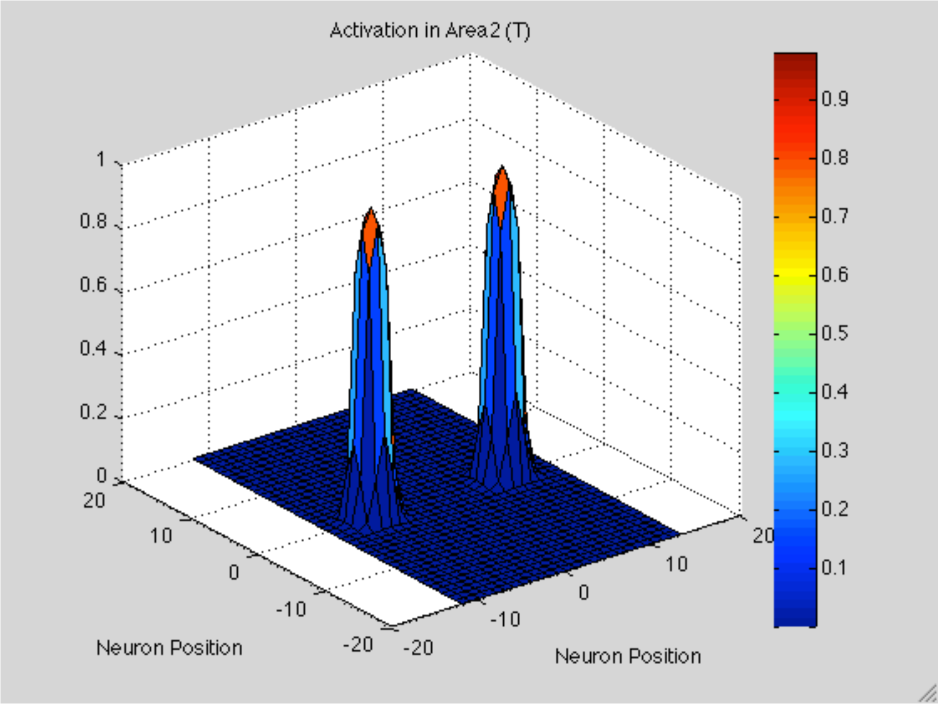


Figure 8.b. 3-D view of the activation pattern. The two peaks of activation are clearly discriminated.

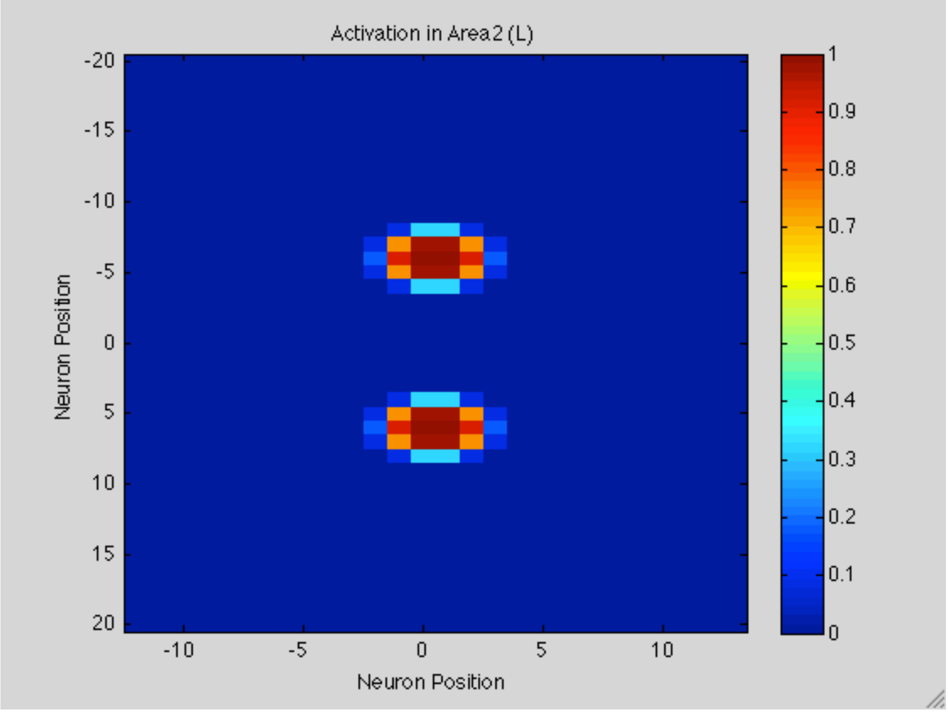


Figure 8.c. Pattern of activation within the higher-level layer if stimuli along the hand are spaced at a distance equal to 3 cm. The edges of the bubbles of activation are much more blurred than those referred to the bubbles within the lower-level layer

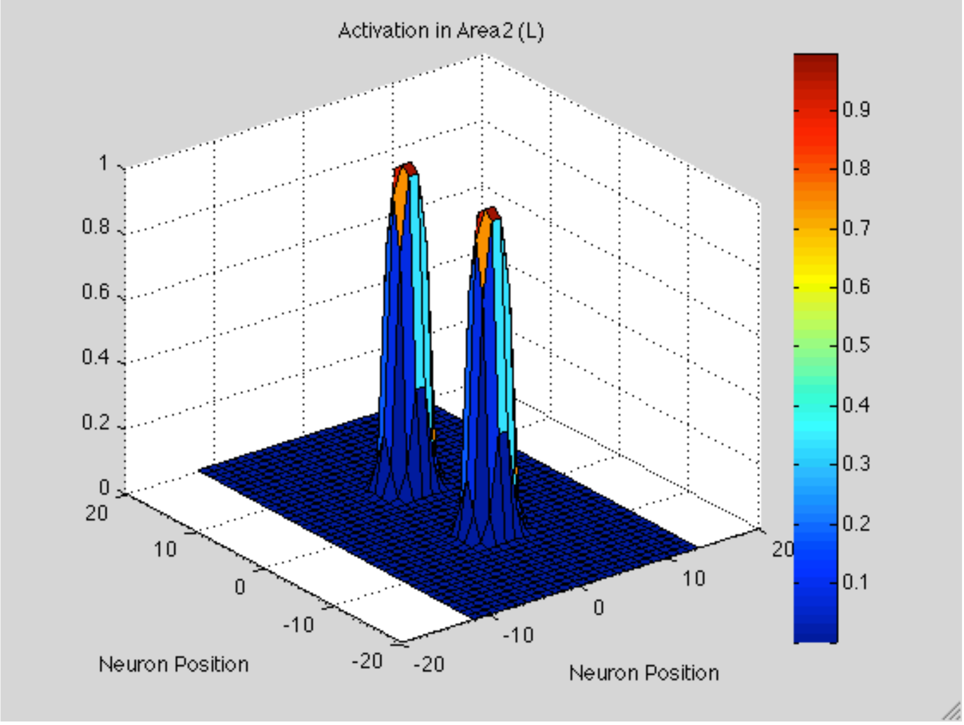


Figure 8.d. 3-D view of the activation pattern. The two peaks of activation are clearly discriminated.

Now, if we compare perceived distance within Area1 and Area2 by considering a transversal stimulation, we can note that the number of neurons between the two bubbles of activation does not change even if bubbles activation strength change slightly from Area 1 to Area 2.

Different considerations arise by observing the results obtained when a longitudinal simulation is provided. In fact, in the second layer there are fewer neurons, along that direction, activated over the specific threshold. It means balls become shrink on this orientation supplying an increment of the gap. Now, 10 neurons encoded for the applied distance along the hand (Area1: 8 neurons; Area2: 10 neurons) whereas the same distance, across the hand, is represented by 13 neurons (at any layer).

This final result provides rescaling within high-level area.

Activation in this level has been computed in the same way of activation within Area1. So, the equations are very similar.

$$\tau \frac{d\chi_{ij}^{s}(t)}{dt} = -\chi_{ij}^{s}(t) + F(u_{ij}^{s}(t)) \qquad \textbf{(2.16)}$$

$$F(u) = \frac{G_{max}}{1 + exp(-\gamma(u - u_0))}$$

Note that *equation 2.16* is not more than a new version of *equation 2.9* in which the apex "*s*" was used.

By solving *equation 2.16* with Euler's method, we can write:

$$\chi_{n+1}^{ij,s} = \chi_n^{ij,s} + \frac{\Delta t}{\tau}\left[-\chi_n^{ij,s} + F(u_n^{ij,s})\right] \tag{2.17}$$

Finally:

$$\chi_{n+1}^{ij,s} = \chi_n^{ij,s} + \frac{\Delta t}{\tau} \cdot \left[-\chi_n^{ij,s} + \frac{G_{max}}{1+exp\left(-\gamma \cdot \left(u_n^{ij,s} - u_0\right)\right)}\right] \tag{2.18}$$

In conclusion in the table below there is a list of parameters value used to implement the network.

Table 1

Receptive Fields of neurons within the Area1
$\Phi_0^f = 1 \quad \sigma_x^\Phi = 0.15\ cm \quad \sigma_y^\Phi = 0.30\ cm$
Lateral Synapses within Area1 and Area2
$L_{ex} = 1.2 \quad \sigma_{ex}^l = 1.40\ neurons$
$L_{in} = 0.8 \quad \sigma_{in}^l = 1.75\ neurons$
Feed-Forward Synapses from Area1 to Are2
$W_0^{f \to s} = 3 \quad \sigma_x^W = 1.70\ neurons \quad \sigma_y^W = 0.85\ neurons$
Sigmoidal Characteristic of Neurons
$G_{max} = 1 \quad u_0 = 12 \quad \gamma = 12$
Time Constant and Simulation Step
$\tau = 3\ ms \quad \Delta t = 0.5\ ms$
External Stimuli
$I_0^{f,T} = I_1^{f,T} = I_2^{f,T} = 1.5 \qquad \sigma_I^{f,T} = 0.1\ cm$

Border Effects and Periodic Domain

The model has been implemented in order to satisfy important considerations. In particular, each neuron within Area1 and Area2 must present the same features. It means that each neuron within the same layer must receive the same number of connections (that is all the neurons must behave equally). In other words, each neuron has to be linked to the same number of neighbourhood. Moreover each neuron in Area2 must be connected to the same number of neurons in Area1. Similar considerations have been made in order to provide input to neurons due to the interaction between RFs and external stimulus. Of course, without introducing some specific artifice, previous requisite is not satisfied by the network, since neurons at the borders receive fewer connections than neurons near the centre of the layers.

Now, we can think about a neuron, which is sitting over the left edge of the lower-level area. As it is well known, a matrix of 41x26 units compose Area1. So, we can consider the neuron in position (21,1). According to the matrix disposition, this neuron is located on the middle of the left edge of the matrix. In other words, it is one of those neurons that stand on the left border of the lower-level area.

So, we are focusing on one of the two orange-painted unit that appear in Figure 9.

It is easy to note that neuron in position (21,1) has not the same number of neighbourhoods that neurons close to the centre of the matrix (here I make a comparison between this neuron and the one in position (21,13)) have.

So, neurons over the border of the matrix or very close to it will receive synapses connection only from one side of the matrix. In this example, (21,1) neuron is linked only to those neurons that stand on its right, because there are not neurons on its left.

Even if they receive a contribution from each unit, synapses represented by Mexican hat configuration or Gaussian function will not provide symmetrical effects in this region of the matrix. In fact, *neurons sitting here receive a stronger inhibition than those on the middle.*

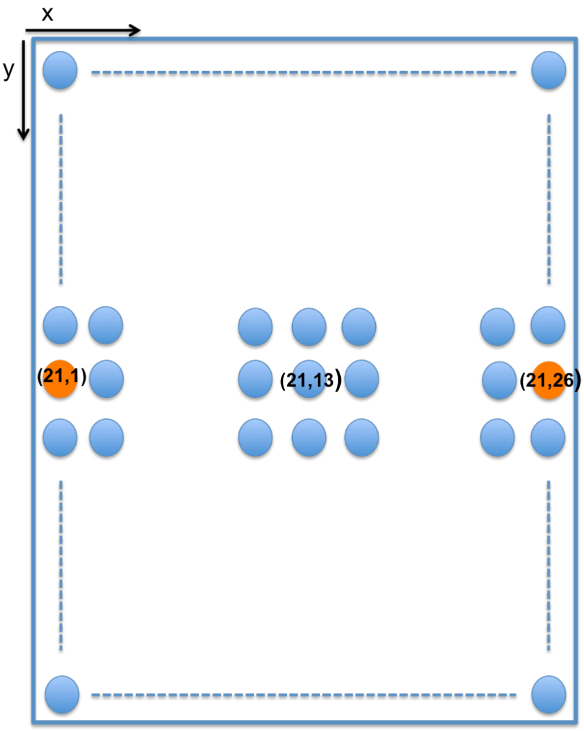


Figure 9. Border Effects. Neurons close to the edge of the cortical area (orange circles in the figure) do not receive the same synaptic contribution of neurons within the center of the cortical area itself.

Simply, (21,1) has fewer neighbourhood and so it receives a lower excitatory effect. Hence, neurons have not the same features.

These undesirable effects are called "*Border Effects*" and they occur near or at the borders of the matrix itself (from the left to right, and from the bottom to the top).

The classical solution adopted in neural network modelling to avoiding this problem, is to implement a *Periodic Domain*

Thanks to Periodic Domain the 41x26 matrix evolved into an endless matrix. This means that each neuron becomes the centre of a virtual matrix, which guarantees symmetrical effects.

Now, (21,1) neuron has the same number of neighbourhood of (21,13) neuron. This consideration is valid for each neuron.

Periodic Domain provides neighbourhoods each neuron needs. So, by considering the example made before, the domain will supply neighbourhoods on the left side of the (21,1) neuron. These neurons are those sitting on the opposite side (right side) of the matrix.
Figure 10 is a good illustration of how the Periodic Domain works.

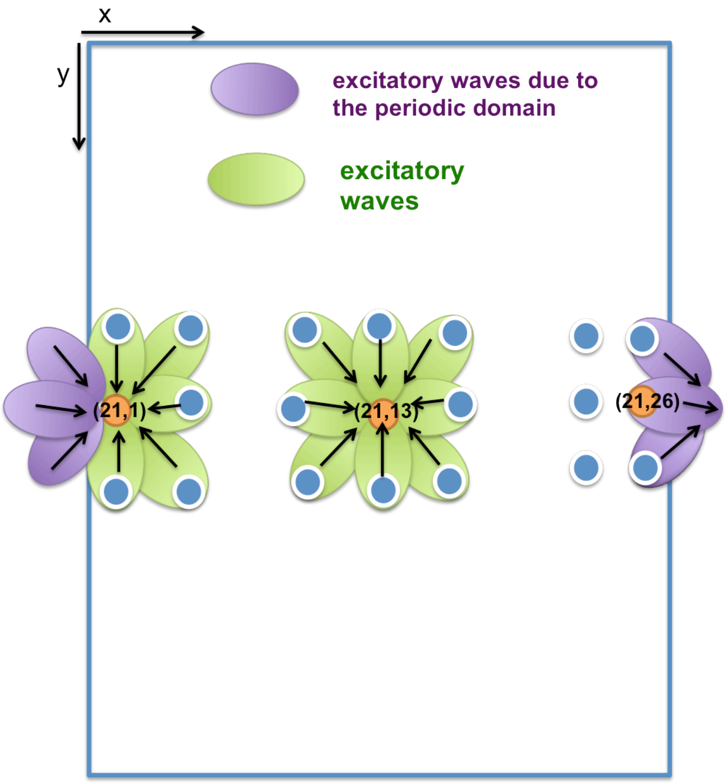


Figure 10. Periodic Domain. Neurons sitting in the border of the matrix receive synapses connection they need from neurons sitting in the opposite side.

So, the algorithm that reproduces Periodic Domain is executed in each part of the model concerning the simulation of external stimuli, receptive fields, lateral synapses and feed-forward synapses.
Two vectors containing the distance values between each neuron are computed. The first one is referred to transversal distances (x axis), the second one to longitudinal distances (y axis).
When the absolute distance is greater than the half size of the matrix, it is set to a lower value in order to reproduce what is illustrated in the picture above.

In formula:

$$D_x^{ij} = \left\{d_{ij,i1} \dots d_{ij,ik} \dots d_{ij,i26}\right\}, \ k = 1,2, \dots \frac{M}{2} \qquad \textbf{(2.18)}$$

where $d_{ij,ik}$ indicates the distance between ij neuron and ik neuron, which is located in the same row but in a different column.
Moreover:

$$\forall k = 1,2, \dots 26 \quad if\left(\left|d_{ij,ik}\right| > \frac{M}{2}\right) \Rightarrow d_{ij,ik} = d_{ij,ik} - \frac{M}{2} \qquad \textbf{(2.19)}$$

Same considerations have been made along y-axis. Obviously, it is necessary to replace M with N.

Chapter 3

Simulation Results

In the following I am going to explain the results obtained by using the model.

In particular, the simulation represents a good approximation of data from *Longo & Haggard Paper* as well as *Green Paper* [*ref. 3, ref. 4*]. This means, orientation-dependent tactile illusion is reproduced according to each consideration found in the articles they have written. In other words, perceived distance changes by considering different orientation.

Moreover, a distort representation of the body inside the brain can increase anisotropy in perceived size of tactile objects and perceive distance as well. For example, if the hand is represented as being longer and more slender than it really is, distances oriented proximo-distally, along the body surface, should feel larger than those oriented medio-laterally, across the body surface. Conversely, if the hand is represented as being wider than it actually is, distances oriented across the hand should be perceived as larger than those oriented along the hand.

In particular by taking a look at Figure 1 (*Normal*) as well as Table 1 and 2 it easy to note that the body model mediating touch presents a dorsum that is stretch along medio-lateral axis. Hand is represented as being wider than it actually is. This would produce the orientation-dependent tactile illusion.

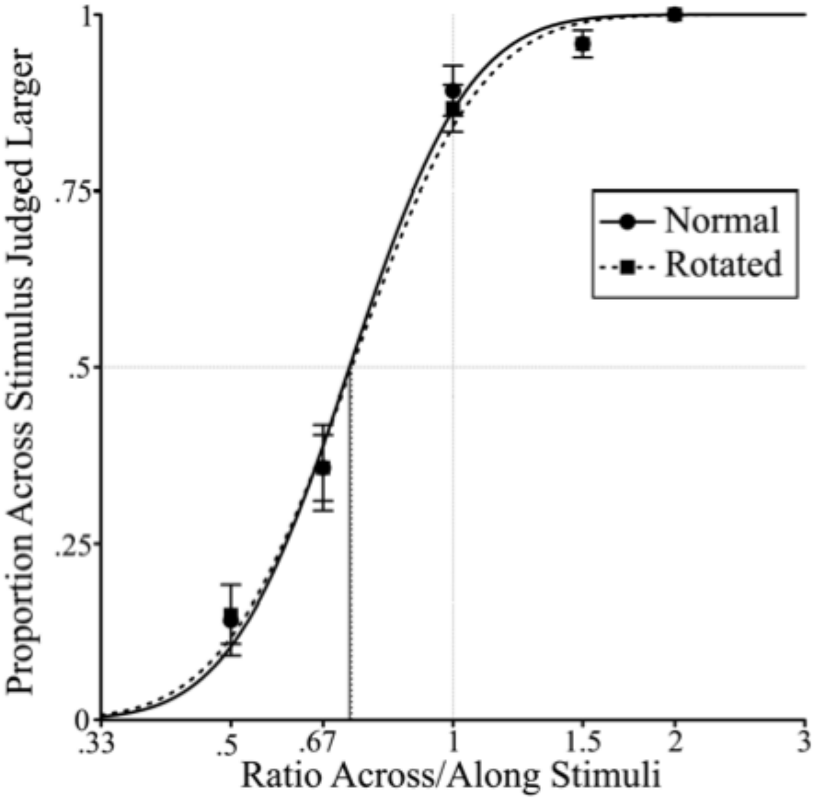


Figure 1. **Results from Experiment 3 conducted by Longo & Haggard. Error bars represent the standard error of the mean. Vertical lines represent points of subjective equality.**

Cumulative Gaussian functions reported in Figure 1, can be described by two important parameters, which are *Point of Subjective Equality* (PSE) and *Interquartile Range* (IQR).
In particular:

- *Point of Subjective Equality* (PSE).

  It represents the Across/Along ratio value at which the Psychometric function crossed 50%. This means that at that ratio, participants gave one response (across stimulus larger than the along one) on the half of the times, and the opposite response (along stimulus larger than the across one) on the other half of the times, i.e., they were responding at chance. In other words, PSE is the ratio for which the two investigated distances are judged as equal (the probability to judge across stimuli as larger it is 0.50).

- *Interquartile Range* (IQR).

  It is a measure of the slope of the psychometric function (i.e., the distance between where the Cumulative Gaussian function crossed 25% and 75%).

Table 1 shows experimental data referred to the *Normal* curve whether Table 2 provides parameters that describe that curve.

Table 1

Longo & Haggard's Data		
Across (cm) / Along (cm)	*Ratios*	*Proportion Across Judged Larger*
2/4	0.5	0.15
2/3	0.67	0.36
3/3	1	0.88
3/2	1.5	0.96
4/2	2	1

Table 2

PSE	*0.25*	*0.75*	*IQR*
0.729	0.593	0.895	**0.302**

It easy to note that PSE differs from 1, that is, PSE = 0.729.

In addition, orientation-dependent tactile illusion has been reported on *Green Paper*. Figure 7 in *Chapter 1* shows that perceived distance is judged depending on stimulus orientation. In particular, by considering any investigated body parts, PSEs values stand within the range 0.64÷0.99 providing a mean value which is equal to 0.84. Moreover, an important consideration, about it, is provided. In fact, as the two linear functions diverge by increasing the size at each orientation, I can say tactile illusion effect becomes higher. So, orientation-dependent tactile illusion is a function of distance running between two stimuli on the skin surface.

However, differences in term of perceived distance between transversal and longitudinal directions are not as significant as expected. In fact, some studies suggest that the long axis of RFs on the hairy skin of the limbs may be more than twice as long as the short axis. By considering only the shape of the RFs, tactile distance along the transversal orientation should be perceived at least twofold bigger than along the longitudinal orientation. But this is not the case. That is, *the illusion is substantially smaller than would be expected on the basis of sensitivity, cortical magnification or RF geometry*. Hence, we can hypothesize that some processes in the brain correct for the distortions characteristic of the somatosensory homunculus and RF shape, although the compensations is only partial.

This behaviour of the brain is called *rescaling*. As the brain is not able to reproduce perfect rescaling, the final result is the Weber's illusion. *Shortly, rescaling decreases Magnification effects.*

So, the model has been built in order to reproduce previous considerations.

Different simulations were performed by stimulating the network by different pairs of stimuli in the across and along orientation, in order to obtain different ratio (across/along) values. In particular two different cases of study are reported. In the first case, for each ratio value, the two distances (along and across) were set so that their mean value (called *Mean Distance Value (MDV)*) was always equal to 3 cm. In the second case, for each ratio value, the two distances (along and across) were set so that the *Mean Distance Value (MDV)*) was always equal to 4 cm. This implies that in the first case study, the distances applied along the two orientations were smaller on the average than the distances applied in the second case study.

Hence I investigated the behaviour of the model by setting ratios that differ from those in Longo & Haggard Paper.

Then, I made a comparison between rescaling effect, as well as tactile illusion effect, in Case 1 and in Case 2. In other words, I can observe how the model rescales perceived distance within Area2 in both 3 cm and 4 cm size but also if tactile illusion increases for distances get larger. Then, I compared the results I have obtained to the data from Green Paper.

The distances that composed the ten different investigated ratios, were obtained by computing a simply equation system.

$$\begin{cases} x + y = 2 \cdot MDV \\ \dfrac{x}{y} = RATIO \end{cases} \tag{3.1}$$

where x is the distance across the hand and y represents that one along the hand.

Table 3 shows ratios and distances along transversal and longitudinal orientation applied in the simulations.

Table 3

Ratios	***MDV = 3 cm (T cm/L cm)***	***MDV = 4 cm (T cm/L cm)***
0.5	2/4	2.67/5.33
0.65	2.36/3.64	3.15/4.85
0.75	2.57/3.43	3.43/4.57
0.8	2.67/3.33	3.56/4.44
0.85	2.76/3.24	3.68/2.32
1	3/3	4/4
1.1	3.14/2.86	4.19/3.81
1.25	3.33/2.67	4.44/3.56
1.5	3.6/2.4	4.8/3.2
2	4/2	5.33/2.67

Note that a MDV equal to 3 cm as well as 4 cm is provided.

A ratio equal to 0.75 indicates that the comparison between 2.57 cm across the hand and 3.43 cm along the hand was investigated if MDV was equal to 3 cm, whereas the comparison between 3.43 cm across and 4.57 along was investigate in case of MDV = 4 cm.

However, each distance value showed in the previous table has been perturbed by Gaussian noise for a better reproduction of the real case. In fact, during an experiment it is impossible to set the gap between the two stimuli at a specific value in a perfect way. This means, the position of each stimulus could differ a little bit from the ideal location reported in the table. Moreover, the stimulus intensity has been perturbed by noise as well. On the overall, the noise applied on the external stimulus accounts both for the environmental noise corrupting the input, and the internal neural noise.

So, the network I have implemented is a stochastic neuronal network and not a deterministic one.

According to the Normal Distribution the random noise was reproduced using the specific Matlab R2009b function. Here, I reported as an example, few rows of the algorithm that set location and amplitude of two stimuli running across the hand spaced by 2 cm.

```
pos_stim_1_T = -1 + (0.15) * randn(1);
pos_stim_2_T= 1 + (0.15) * randn(1);
forza_in_1_T = 1.5 + (0.15) * randn(1);
```

The function *randn(1)* generates a value from a Normal Distribution with mean (1 cm, -1 cm, 1.5 cm respectively) and standard deviation equal to 0.15 cm. Note that -1 and 1 are the ideal locus stimulus whether 1.5 is the amplitude of the stimulus.

Since each external stimulus was affected by noise, I considered 100 trials for each ratio. That is, I investigated any case of study with 1000 comparison.

Finally, a curve representing the proportion of across stimuli judged larger than longitudinal stimuli has been computed for each ratio (and for case study 1 and case study 2) for both Area1 and Area2. As extensively described in Chapter 2, the distance read out by the network has been codified in terms of number of neurons separating two peaks of activations. So, at each ratio, the response of the network was interpreted as “across stimulus larger than along stimulus” if the number of neurons separating the peak of activation in case of across stimulation was higher than the number of neurons separating the peak of activation in case of along stimulation.

As in Figure 1, the curve represents a Cumulative Gaussian function, which was fit to each data with least-squares regression using R 2.8.0. (a software devoted to statistical analysis of data).

In the following, presentation of results is organized in seven different sections for the sake of clarity.

1. Case study 1: Mean Distance Value is equal to 3 cm.

Considering a Mean Distance Value equal to 3 cm, the network provided results showed in Table 4.

Table 4

		AREA 1	*AREA 2*
MDV = 3 cm (T cm/L cm)	*Ratios*	*Proportion Across Judged Larger*	*Proportion Across Judged Larger*
2/4	0.5	**0**	**0**
2.36/3.64	0.65	**0.05**	**0**
2.57/3.43	0.75	**0.42**	**0.14**
2.67/3.33	0.8	**0.55**	**0.23**
2.76/3.24	0.85	**0.74**	**0.41**
3/3	1	**0.95**	**0.8**
3.14/2.86	1.1	**0.96**	**0.92**
3.33/2.67	1.25	**1**	**1**
3.6/2.4	1.50	**1**	**1**
4/2	2	**1**	**1**

At any trial the gap between the two stimuli (in both across and along orientation) was computed as number of neurons (see Chapter 2).

Suppose to analyse a ratio equal to 0.75; by comparing results in Area1 to those in Area2 at this specific ratio it easy to note the model provides different outputs. The proportion of transversal stimuli judged larger than longitudinal stimuli is higher in Area1 than in Area2. In fact, 42 out of 100 trials gave that response within the first layer, whether the same response is given in Area2 by no more than 14 trials.

In general, from the range ratio 0.65÷1.1, results are different between Area1 e Area 2. Lower values in Area2 indicate that there are fewer trials in which a positive response (across judged larger) has been found. This demonstrates that behaviour in Area 2 is more reliable, that is the model has reduced the illusion that the across stimulus is larger than the along one (in other words. the model has increased the gap between stimuli along longitudinal direction).

This interesting conclusion proves the model integrates input coming from Area1 in order to implement rescaling.

Finally, the Cumulative Gaussian function was fit to each data with least-squares regression (see Figure 2). The x-axis is in a logarithmic scale.

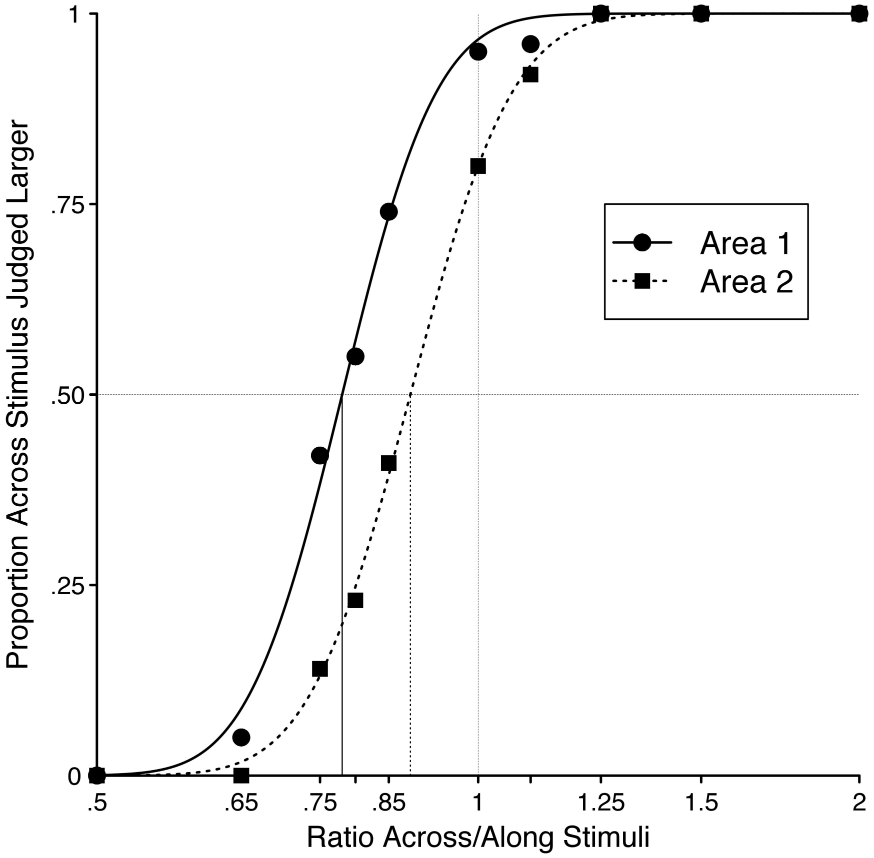


Figure 2. Simulation results. MDV is equal to 3 cm. Rescaling effect as well as orientation-dependent tactile illusion is reproduced.

Note that vertical lines represent Point of Subjective Equality.

In particular:

Table 5

	PSE	*0.25*	*0.75*	*IQR*
AREA1	**0.781**	0.713	0.856	0.143
AREA2	**0.884**	0.801	0.976	0.175

This result clearly demonstrates the curve relating to Area2 is shifted more on the right highlighting rescaling effect. In fact, if rescaling is not provided, output within Area2 should be equal to that one within Area1. It is possible to compute the amount of rescaling shifting from Area 1 to Area 2 by simply subtracting the PSE value referred to Area1 to the PSE value of Area2.

Moreover, taking a closer look at Figure 1 it easy to note that the model reproduces the orientation-dependent tactile illusion. If there is no distortion of hand shape, PSE_{Area2} should equal to 1 indicating that stimulus orientation does not bias perceived size. In other words, when the across and along size are the same (ratio equal to one) the output from Area2 should be, on average, equal to 0.5. In this way, the ideal curve (no tactile illusion) should be described by a step function with a mean value equal to 1.

The figure below reports illustrative explanation about what rescaling as well as orientation-dependent tactile illusion are.

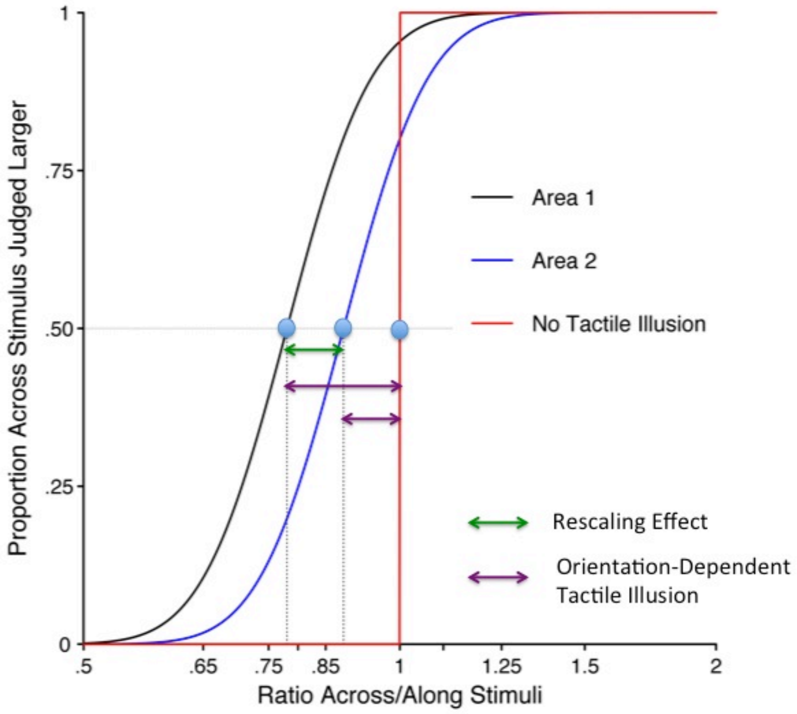


Figure 3. Rescaling effect is due to the difference between PSE_{Area2} and PSE_{Area1} whereas tactile illusion is due to the difference between 1 and $PSE_{Area1/2}$.

So, in this case of study, there is a clear bias in both lower-level layer and higher-level layer for the across stimuli to be judged larger than the along stimuli.

In particular, there is much more bias within Area1, and the bias is reduced in Area 2.

As for rescaling effect, it is possible to compute the amount of illusion simulated by the neuronal network. This is equal to the difference between 1 (PSE value in case of no tactile illusion) and PSE_{Area2} (see Table 5).

Table 6

PSE_{Area1}	PSE_{Area2}	Rescaling Effects Magnitude (PSE_{Area2} - PSE_{Area1})	Orientation-Dependent Tactile Illusion Magnitude (1- PSE_{Area2})
0.781	0.884	0.103	0.116

$$Rescaling\% = \frac{(PSE_{Area2} - PSE_{Area1}) \cdot 100}{1 - PSE_{Area1}} \qquad (3.2)$$

It is possible to compute the Rescaling effect as a percentage of the tactile illusion. Here we can say rescaling cover the 47.03% of the bias presents in Area1

Moreover, due to a lower IQR, Area1 presents a greater precision than Area2 because data are spread in a tiny values range.

So, IQR can be interpreted not only as a measure of the slope of each curve, but also as a measure of how much the simulation data are consistent. Hence, the greater is the IQR value, the more consistent is the model. Anyway, IQR in both first and second layer is about the same. Therefore, the curves fit data with a good precision and it is clearly lower than the ideal case.

As I wrote in Chapter 2 rescaling effect is provided by the model increasing the gap between stimuli along proximo-distal orientation and preserving the gap on the transversal direction. This mean that in Area2 the number of neurons sitting between the two balls of activation should increase (comparing to Area1) in the along orientation, whereas it has to remain the same in the transversal orientation.

It is possible to check it observing Table 6.

At any ratio and any trials too, the perceived distance (number of neurons composing the gap) within Area1 and Area2 was computed in both case of transversal and longitudinal orientation. Then, the difference between them was found. In this way a difference vector of 100 values was provided for each ratio. Finally I computed the percentage of changing (%C) as well as the mean changing value (MCV). %C is related to the number of trials, which did not preserve the perceived distance from Area1 to Area2, whereas MCV indicates the mean value related to the changing.

Both %C and MCV were computed at any investigated orientation.

For a better understanding I have reported a scheme referred only to the first ten trials of the first investigated ratio (0.5).

1) *Perceived Distance computed within Area1.*

Transverse									
9	11	10	10	11	11	11	10	11	12

Longitudinal									
19	19	19	17	18	16	17	19	19	17

2) *Perceived Distance computed within Area2.*

Transverse									
10	11	10	10	11	11	12	11	11	12

Longitudinal									
23	21	20	18	20	18	19	21	24	19

3) *Difference Vectors were computed as absolute differences of the vectors at the points 1 and 2.*

Transversal Difference									
-1	0	0	0	0	0	-1	-1	0	0

Longitudinal Difference									
-4	-2	-1	-1	-2	-2	-2	-2	-5	-2

4) *Computation of %C and MCV.*

	Across	Along
% Changing	30%	100%
Mean Changing Value (Neurons)	-1	-2.3

Table 7

	Across	Along
% Changing	47%	100%
Mean Changing Value (Neurons)	-1	-2.51

Along the transversal direction, perceived distance differs no more than one neuron (*we can assume that there are no significant changing in term of number of neurons from Area1 to Area2*). Moreover, only few trials did not preserve the perceived distance from the first layer to the second one. Instead, along the hand perceived distance changes more than 2 neurons. So, the assumption about rescaling is verified.

2. Case study 2: Mean Distance Value is equal to 4 cm.

In the second case study, perceived distance was investigated considering a MDV equal to 4 cm.

Comparing this case to the first one, similar conclusions have been found.

Simulation results are shown in Table 8.

Table 8

		AREA 1	*AREA 2*
MDV = 4 cm (T cm/L cm)	*Ratios*	*Proportion Across Judged Larger*	*Proportion Across Judged Larger*
2.67/5.33	0.5	**0**	**0**
3.15/4.85	0.65	**0.03**	**0.01**
3.43/4.57	0.75	**0.36**	**0.13**
3.56/4.44	0.8	**0.57**	**0.19**
3.68/2.32	0.85	**0.89**	**0.55**
4/4	1	**0.96**	**0.91**
4.19/3.81	1.1	**0.99**	**0.99**
4.44/3.56	1.25	**1**	**1**
4.8/3.2	1.50	**1**	**1**
5.33/2.67	2	**1**	**1**

As in the first case of study, by comparing patterns from lower-level layer and higher level-layer, it easy to note that in Area 2, the illusion that the across stimulation is larger than the along one is reduced. That is, the model has increased the gap between stimuli along longitudinal direction. Hence, there are fewer trials with a positive response in Area 2 compared with Area 1.

The Cumulative Gaussian function is shown in Figure 4.

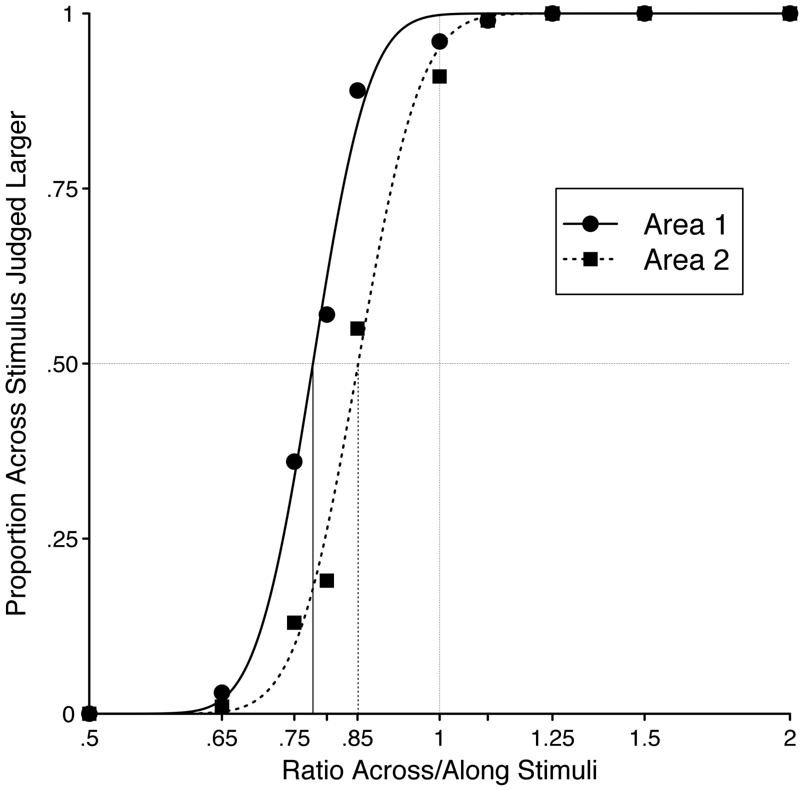


Figure 4. Simulation results. MDV is equal to 4 cm. Rescaling effect as well as orientation-dependent tactile illusion is reproduced.

Observing the picture, we can note there is less rescaling in the case of 4 cm MDV than 3 cm MDV. In fact, the two curves are closer to each other. Moreover, the model provides a better precision since the slope is clearly higher (even if it is still lower than the ideal case). Data referred to the curves are reported below.

Table 9

	PSE	*0.25*	*0.75*	*IQR*
AREA1	**0.778**	0.733	0.826	0.092
AREA2	**0.851**	0.797	0.909	0.112

Differences in PSE demonstrate the neuronal network rescales perceived distance from Area1 to Area2.

Inter-Quartile Ranges demonstrate curves have different slope and also a better precision on the Cumulative Gaussian Function referred to Area1.

Finally, Table 9 reports both the Rescaling Effects Magnitude and the Orientation-Dependent Tactile Illusion Magnitude.

Table 10

PSE_{Area1}	PSE_{Area2}	Rescaling Effects Magnitude (PSE_{Area2} - PSE_{Area1})	Orientation-Dependent Tactile Illusion Magnitude (1- PSE_{Area2})
0.778	0.851	0.073	0.149

Proportion 3.2 suggests rescaling effect covers 32.88% of the tactile illusion within Area1.

Now, by comparing data in Table 10 with data in Table 6, we can obtain interesting information. In fact, in this case of study, Rescaling Effects Magnitude is lower than it is in the first case.

Moreover, Orientation-Dependent Tactile Illusion Magnitude is higher because of greater bias. In fact, by comparing Cumulative Gaussian functions referred to Area2 in both cases of study, it easy to note there is more bias in Case 4 for across stimuli to be judged larger than along stimuli.

In addition, according to Green Paper, these results demonstrate perceived distance is a function of the real distance over the skin surface.

So, the model provides (data are different from those reported by

Green at his case of study) qualitatively similar results as those obtained by Green. The output of the neuronal network changes if distance over the skin changes. *There are not only differences in term of orientation but also in term of size of applied distance.* Anyway, I am going to explain it better in the paragraph "*Comparison between Area2 outputs by considering different Mean Distance Value*".

As in Case 1, assumption about rescaling has been investigated by computing AVG_T and AVG_L (see Table 11).

Table 11

	Across	**Along**
% Changing	36%	100%
Mean Changing Value (Neurons)	-1	-2.57

So, the assumption about rescaling is verified.

Note that in both Case 1 and Case 2, the model provides a PSE, in the second layer, which is significantly less than 1. Then, according to Longo & Haggard Paper, the model simulates a bias to represent the hand as wider than it really is. *That is, tactile stimuli running medio-laterally are systematically reproduced as larger than stimuli running proximo-distally.*

3. Comparison between Area1 outputs by considering different Mean Distance Value.

What happens within Area1 simply by considering different MDV?

Point of Subjective Equality and Inter-Quartile Ranges referred to Area1 preserve about the same values in both Case 1 and Case 2.

In particular:

$$PSE_{Area\ 1}^{Case\ 1} - PSE_{Area\ 1}^{Case\ 2} = 0.781 - 0.778 = 0.003 \qquad \textbf{(3.3)}$$

$$IQR_{Area\,1}^{Case\,1} - IQR_{Area\,1}^{Case\,2} = 0.143 - 0.092 = 0.051 \qquad (3.4)$$

It is known IQR is related to the slope of a curve. Since difference 3.4 is close to 0, we can assume slopes of Cumulative Gaussian functions are about the same in both Case 1 and Case 2.

Moreover, difference 3.3 is almost null, as $PSE_{Area\,1}^{Case\,1}$ and $PSE_{Area\,1}^{Case\,2}$ have similar values.

So, it is expected the two curves are about identical.

In other words, the two curves should have the same bias value.

What I have just written is reflected in the output of Area1. In fact, the proportion of across stimulus judged larger is about the same in both Case 1 and Case 2 (see Table 4 and Table 8 respectively).

Figure 5 shows the comparison.

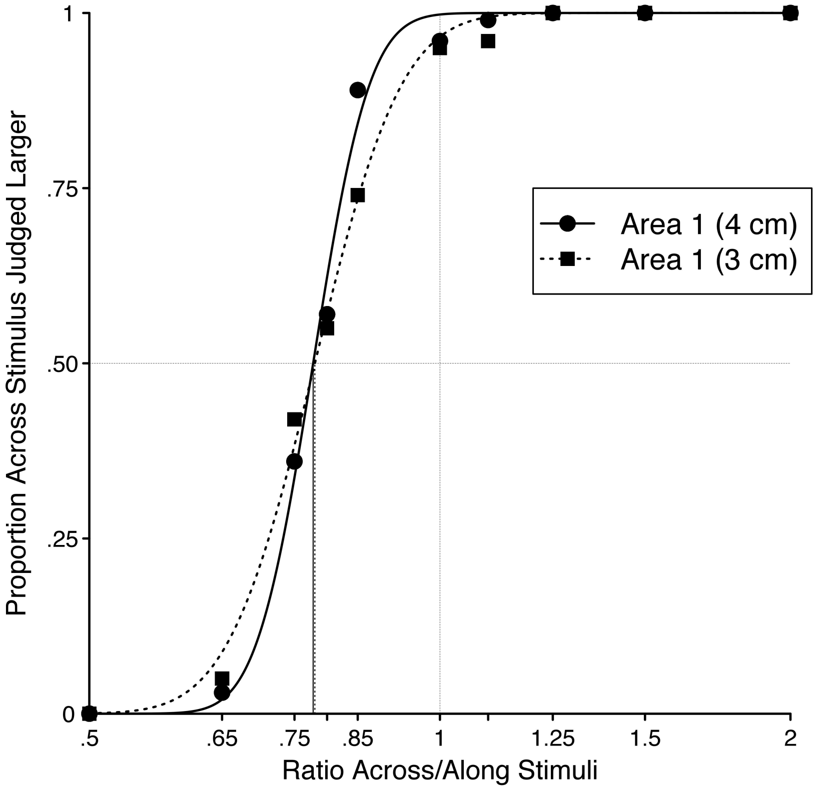


Figure 5. **Area1 outcomes in both 3 cm and 4 cm cases. Note that there are no rescaling effects by simply changing the size of applied distance.**

Note there are no noticeable differences between the two curves.

This final result is very interesting. In fact, it suggests us, *there is not a relationship between perceived distance and the size of applied distance (Green discussion) within Area1, that is, there are no rescaling effects here, by simply changing the size of applied distance*. As a consequence, PSEs are about the same.

So, as expected, the neuronal network does not provide rescaling in in the first-layer where orientation-dependent tactile illusion is present and does not depends on the size (same bias). We can assume the tactile illusion is the same in both 3 cm and 4 cm cases. So, what Green found in his studies is not observable in Area1 of the network. Nevertheless, results by Green are referred to perceived distances, which are assumed to be the output elaborated in the neuronal network by the second layer (Area2).

In conclusion, both Green consideration and orientation-dependent tactile illusion should be reproduced by the model as the output of Area 2.

4. Comparison between Area2 outputs by considering different Mean Distance Value.

This comparison indicates that the model can reproduce results by Green.

From Green's data, one can conclude that perceived tactile distance depends on both the body locus and the orientation of stimulation, and that *the size of the orientation effect depends upon the locus*.

In particular, observing Figure 7 reported in Chapter 1, one could note that there is a tendency for longitudinal judgments to be smaller than transverse judgments. *This effect becomes higher by increasing the applied distance. This means our brain provides a greater tactile illusion for long distances than short ones*. If that kind of effect is reproduced by the neuronal network, two non-overlapping Gaussian Cumulative function should be expected by the comparison between 3 cm and 4 cm Mean Distance Value. Above all, curves should be similar and non-overlapped, that is, the 4 cm MDV curve have to be more on the left side of the chart than the 3 cm MDV curve. This proves that there is a higher orientation-dependent tactile illusion for long distances than short distances just because the difference value between 1 (PSE value if no orientation-dependent tactile illusion is expected) and PSE related to 3 cm MDV is smaller than the difference between 1 and PSE related to 4 cm MDV.

As before I computed the differences in term of PSE and IQR.

$$PSE_{Area\ 2}^{Case\ 1} - PSE_{Area\ 2}^{Case\ 2} = 0.884 - 0.851 = 0.033 \qquad \mathbf{(3.5)}$$

$$IQR_{Area\ 2}^{Case\ 1} - IQR_{Area\ 2}^{Case\ 2} = 0.175 - 0.112 = 0.063 \qquad \mathbf{(3.6)}$$

Once again, difference in term of IQR is very small demonstrating curves have got a similar slope value.

Comparing *difference 3.5* to *difference 3.3* we can note difference within Area2 is ten times bigger than difference within Area1. Although *difference 3.5* is small, it is sufficient to demonstrate the two Gaussian Cumulative functions are not overlapped. Moreover, a comparison between pattern in Area2 in Case 1 and Case 2 can be a good support of what I have declared. In fact, at each ratio (excepted for the ratio equal to 0.5 in which there is the same outcome), *proportion across stimulus judged larger* is higher in the case of 4 cm MDV.

Figure 6 shows the patterns of results from Area2 obtained with the model in both Case 1 and Case 2.

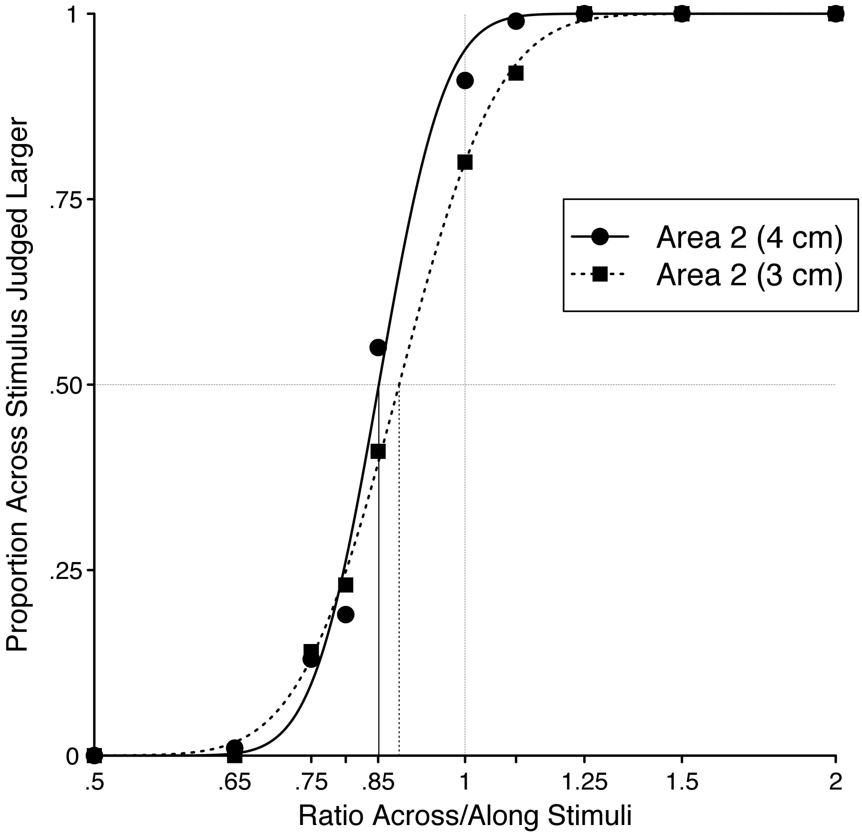


Figure 6. Patterns of results from Area2 obtained with the model in both Case 1 and Case 2. Considerations from Green Paper are verified.

Hence, the higher is the size of the applied distance, the greater is the bias for the tactile stimuli running medio-laterally to be judged larger than stimuli running proximo-distally.

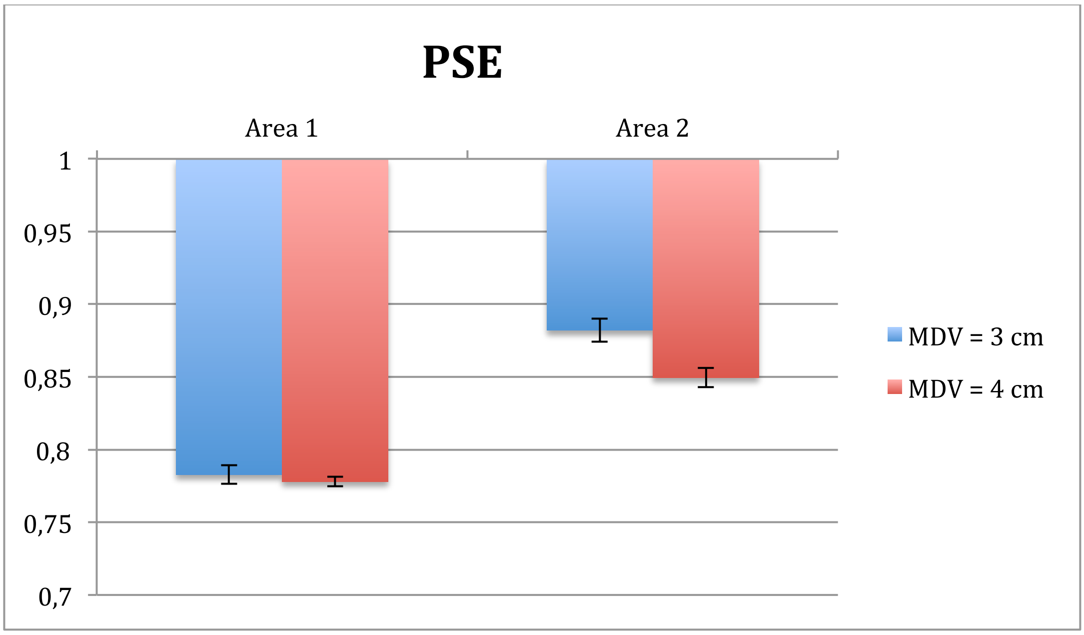
According to the theory, the model reproduces rescaling only on Area2. So, the pattern from Area 2 demonstrates the neuronal network improves the distorted body model created within Area1.

Moreover, considerations from Green Paper are verified.

The paragraph "*Green considerations*" will provide further information about it.

Finally, the following histogram is a useful representation of the model results. Blue columns indicate that a MDV equal to 3 cm was analysed whether red columns are related to the 4 cm MDV.

Note that the height of each column represents the amount of orientation-dependent tactile illusion (within both Area1 and Area2) whether the difference, in term of height, between columns of Area1 and Area2 referring to a specific MDV indicates rescaling process.



The black vertical lines on the top of the columns represent the *Standard Error* (SE) of each data distribution (SE was computed due to equation 3.10 in t-Test paragraph). SE has been computed in order to perform t-Test between simulation results (see *t-Test* paragraph).

5. Green considerations

The paper of the Green reported that linear functions fit data at any investigated body part.

Focusing on the arm, the relationship between perceived distance and applied distance, in both orientations, is given by the following equations:

$$y = 0.81 \cdot x - 0.09 \qquad (Transverse) \qquad \mathbf{(3.6)}$$

$$y = 0.48 \cdot x - 0.18 \qquad (Longitudinal) \qquad \mathbf{(3.7)}$$

where y indicates the perceived distance in assess according to a qualitative scale (*Points*). In fact, subjects were asked to assign numbers to represent the apparent distance between two simultaneous tactile stimuli (subjects were urged to avoid units of inches or centimetres and received practice in assigning numbers to visual distances) whether *x* is the space running between the two stimulation points.

Perceived distance related to the two pair of stimuli spacing at 3 cm and 4 cm respectively is shown in Table 13.a and Table 13.b for both investigated orientation.

Table 12.a

	MDV = 3 cm	***Perceived Distance (points)***
Across	3	2.34
Along	3	1.62
Ratio	1	1.44
Difference	0	0.72

Table 13.b

	MDV = 4 cm	***Perceived Distance (points)***
Across	4	3.15
Along	4	2.1
Ratio	1	1.5
Difference	0	1.05

Note that *Difference* related to a Mean Distance Value equal to 4 cm is greater than that one referred to a 3 cm Mean Value Distance. Moreover, the ratio is higher. As I wrote before, this is a clear demonstration of the fact that the higher is the size of applied distance the higher is the difference in term of judgment between longitudinal and transverse orientation.

For this particular ratio (=1), the neuronal network shows two different values in term of proportion across stimulus judged larger. In particular:

Proportion Across Stimulus Judged Larger (MDV = 3 cm) → ***0.8***

Proportion Across Stimulus Judged Larger (MDV = 4 cm) → ***0.91***

Data are referred to Area2.

This means, there is less orientation-dependent tactile illusion on the 3 cm Case. In fact, a lower proportion indicates fewer trials have presented the positive response.

Anyway, this is only a comparison between two different sizes.

In order to check if simulation results could reflect the Green consideration I investigated the behaviour of the deterministic model with several sizes (see Figure 8). In particular, final results were provided thanks to 20 trials each investigated distance. This is very important because the position of each stimulus is affected with Gaussian noise.

Obviously, a ratio equal to one by comparing transverse and longitudinal size has been considered.

The neuronal network provided a linear relationship between physical distance and perceived distance as reported in “The perception of distance and location for dual tactile pressures”.

Figure 7 shows the relationship between inputs (Applied Distances) and output (Perceived Distances) of the model. The picture was obtained by using Matlab R2009b.

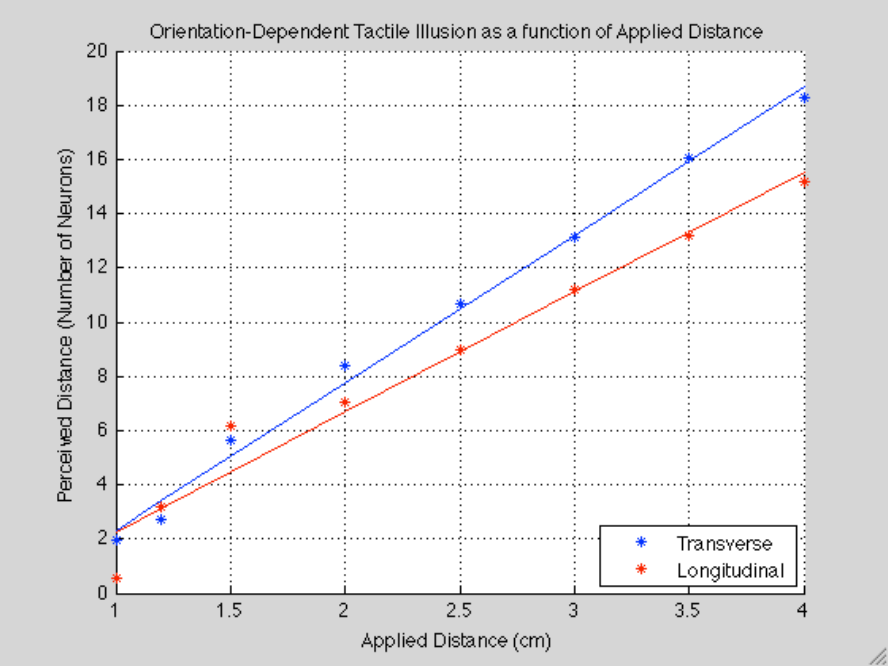


Figure 7. The higher is the applied distance the higher is the orientation-dependent tactile illusion effect. Green considerations are satisfied.

The stars indicate the mean value at any investigated distance. Nevertheless, perceived distance is reported in Number of Neurons and not in "*Points*" such as what is reported on Green paper.

It is impossible to find a correlation between judgments from subjects (Points) and the response of the neuronal network (Number of Neurons). This is why only a qualitative analysis, concerning the topic, has been studied.

The Linear function that fits data from the model was computed and reported below:

$$y = 5.45 \cdot x - 3.15 \qquad \text{(Transverse)} \qquad \mathbf{(3.8)}$$

$$y = 4.42 \cdot x - 2.16 \qquad \text{(Longitudinal)} \qquad \mathbf{(3.9)}$$

where y indicates the Number of Neurons sitting between the two balls of activation, and x is the space running between the two points of stimulation.

Taking a look at both the figure and the equations it easy to note the network provides a greater discrimination of perceived distance along both orientations for size gets larger. According to Green experiment, *linear functions diverge by increasing applied distance*.

The only qualitative comparison I have considered concerns the slopes of the linear functions that fit Green data and linear functions that fit data from the neuronal network.

Looking back at Equation 3.6 and 3.7 (describing Green's data) it easy to note that the slope referred to the transversal orientation is higher than the longitudinal one. In particular, focusing on the ratios of them:

$$\frac{slope_T}{slope_L} = \frac{0.81}{0.48} = 1.69$$

which is clearly greater than one.

Now, we can compare this ratio with that one referred to the slopes obtained by the model, that is:

$$\frac{slope_T}{slope_L} = \frac{5.45}{4.42} = 1.23$$

The ratio is higher than one. Obviously, only a qualitative comparison between the two ratios can be analysed because we cannot compare judgments in term of points with judgments in term of number of neurons. So, I think that what is important is that the model provides a ratio which is greater than one according to the Green Paper.

Now, an interesting theory can be drawn by observing what has been found in the last three sections.

In fact, Section 4, clearly demonstrates that the higher is the applied distance the higher is the tactile illusion. This is the same conclusion of Green Paper. Moreover, Section 3 as well as Section 4 suggests *the higher is the applied distance the lower is the rescaling effect.* Hence, thanks to the simulation result I can conclude that *there is a greater orientation-dependent tactile illusion by increasing applied distance because of less rescaling effect.*

6. Two-point discrimination threshold

Thanks to Longo & Haggard, and Green data another important consideration has been deduced. It is well known there is a better spatial resolution along medio-lateral direction than along proximo-distal one, on the dorsum of the hand. This suggested me to investigate the two-point discrimination threshold reproduced by the model in both along and across orientation.

As I wrote in Chapter 1, the two-point discrimination threshold is the minimum distance between two detectable stimuli. It varies from body region to body region and it depends on the size of the receptive fields and the innervation density of mechanoreceptors in the superficial layers of the skin.

In addition, studies conducted by the authors above suggest two-point discrimination threshold not only varies from body region to body region [*ref. 7*] but also by considering different orientation over a certain skin surface. However there are no studies as concerning this specific aspect. It is really unknown what is the value of the threshold along and across the hand.

Anyway, it is licit to suppose that it is greater across the hand.

The first values in the last two columns of Table 14 represents the threshold simulated by the model. As expected, there is a better discrimination across the hand, which means a greater two-point discrimination threshold.

In fact, the neuronal network provides two unpaired balls of activation if the gap between two external stimuli sitting across the hand is greater than or equal to 1 cm. Conversely, an applied distance equal to 1.2 cm had to be provide in order to guarantee two balls of activation along the hand.

Here we can note that the simulation results are the same across the hand if distances equal to 1 cm and 1.2 cm are investigated. Nevertheless, these distances differ only 2 mm, that is, they are very similar and this is why the model cannot reproduce different values in term of number of neurons. Anyway, the neuronal network can discriminate the two applied distances along the hand. In fact, a big ball of activation will be the final output if stimuli along the hand are spaced by 1 cm whether two distinct balls of activation represent the outcome when an applied distance equal to 1.2 cm is set.

Let’s investigate what happens within Area1 and Area2 considering both 1 cm case and 1.2 cm case.

Transversal two-point discrimination threshold: 1 cm.

If a pair of stimuli is applied on the dorsum of the hand spacing by 1 cm, the output of the neuronal network referred to the lower-layer level is shown in Figure 9.a.

There are two balls of activation clearly spaced by neurons not enough activated (their activation values are lower than the activation threshold). In particular, the gap we are considering is composed by 3 neurons. So, within Area1, a real distance on the skin equal to 1 cm is coded by 3 neurons. Note that this result is also the output of the Area 2 (see Table 14).

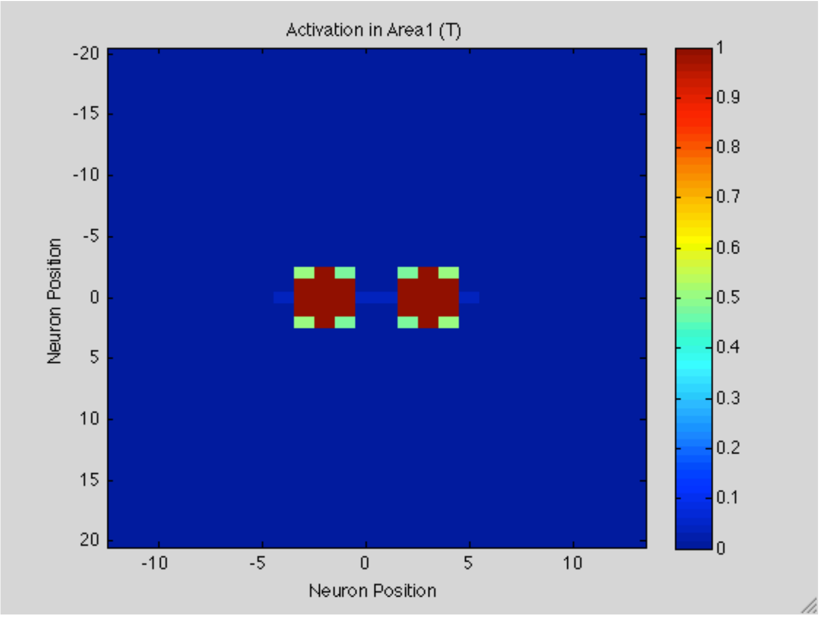


Figure 8.a. 1 cm across the dorsum of hand is the minimal detectable distance within Area1. Bubbles of activation are spaced by 3 neurons.

Applied Distance = 1 cm.

*Output from Area1 = **3** Neurons.*

The two balls of activation are clearly discriminated.

I cannot say the same as concern the outcome from the same layer when the along orientation is investigated. In fact, the pattern is a big ball of activation, that is, the two stimuli are elaborated as only one, spreading from locus to locus of each stimulus.

Figure (9.b) shows what I have declared.

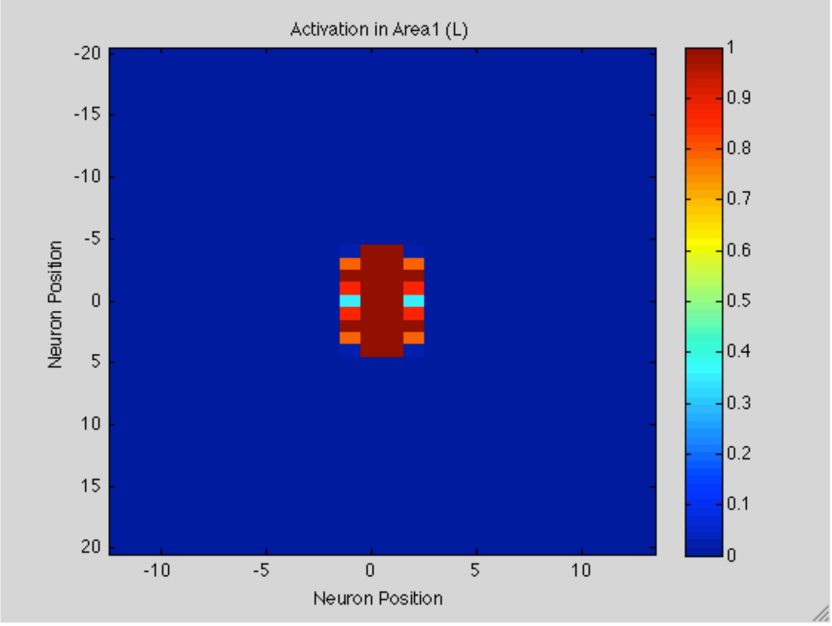


Figure 9.b 1 cm along the dorsum of hand is not detectable within Area1. There is only one big bubble of activation.

Applied Distance = 1 cm.

Output from Area1 = ***0*** *Neurons.*

In the figure above is impossible to discriminate the two balls of activation. Maybe we can only hypothesize where the centre of each ball is. For sure, neurons sitting between them present the maximal activation value.

Now, it is important to observe what happens within Area2 because it represents *the final output of the network as well as the perceived distance*.

Figure 10.a and Figure 10.c are referred to activation in Area2 considering both medio-lateral and proximo-distal direction.

So, by comparing the results within Area2 to those within Area1 as concern the transversal case, it easy to note that the two balls of activation are less discriminated in Area2 but still noticeable. In other words, neurons running between them have got a higher activation value. However, it is still lower than the threshold of activation. That is why it is possible to discriminate 1 cm over the skin surface.

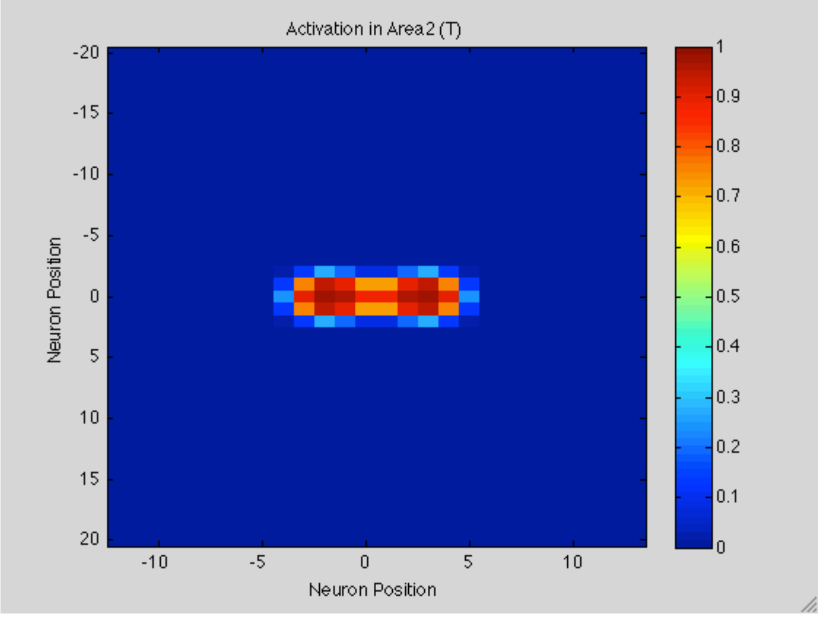


Figure 10.a. Bubbles of activation are less discriminable than those within Area1. Anyway, 1 cm across the hand is still detectable.

Applied Distance = 1 cm.

*Perceived Distance = **3** Neurons.*

What I have just written could be much clearer by having a look at Figure 10.b.

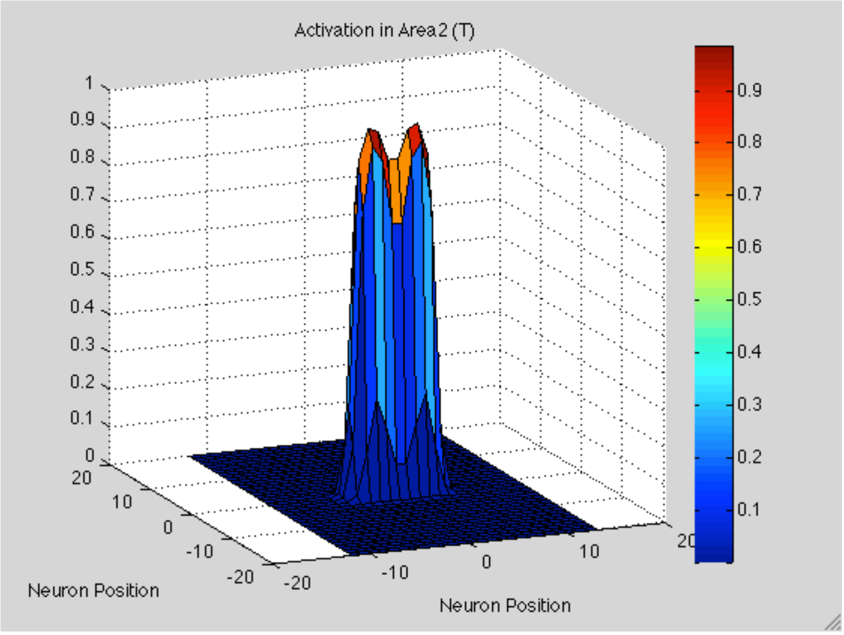


Figure 10.b. 3D representation of Figure 10.a

The figure is a 3D representation of Figure 10.a.

Neurons sitting between the two balls have an activation value within the range 0.8÷0.89 whether the activation threshold is equal to 0.9. The same output is not provided if 1 cm distance is investigated along the hand. In fact, by comparing Figure 9.b with Figure 10.c (below) it is clear to note that in Area2, the activation of those neurons sitting between the centres of the balls of activation is not as high as the activation of those neurons within Area1. However, in Area2 there is still only one ball of activation. Neurons locating from centre to centre of each hypothetical bubble of activation present values within the range 0.97÷0.98, which are clearly higher than 0.9. This is why a distance equal to 1 cm is not noticeable along the dorsum of the hand.

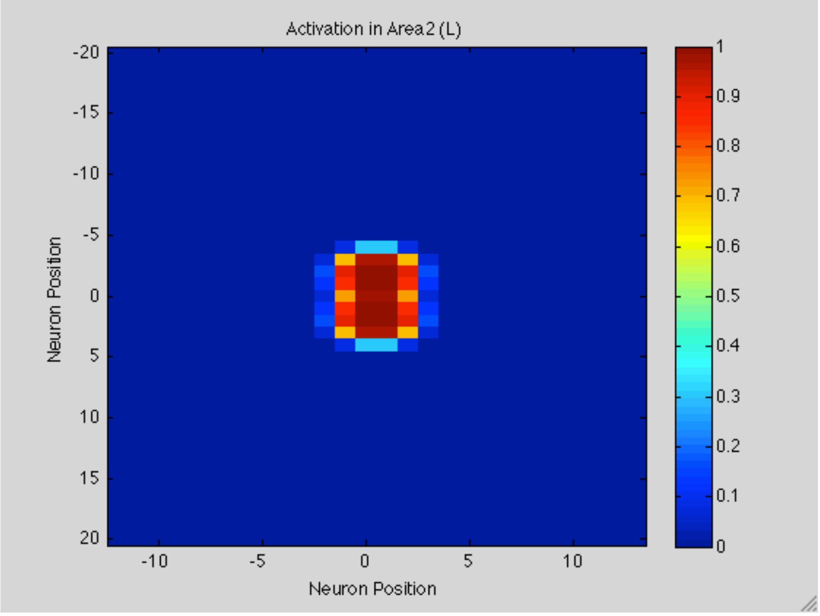


Figure 10.c. Bubbles of activation are more discriminable than those within Area1. Anyway, 1 cm along the hand is not detectable.

Applied Distance = 1 cm.

Perceived Distance = ***0*** *Neurons.*

Finally, Figure 10.d is a 3D representation of the previous picture.

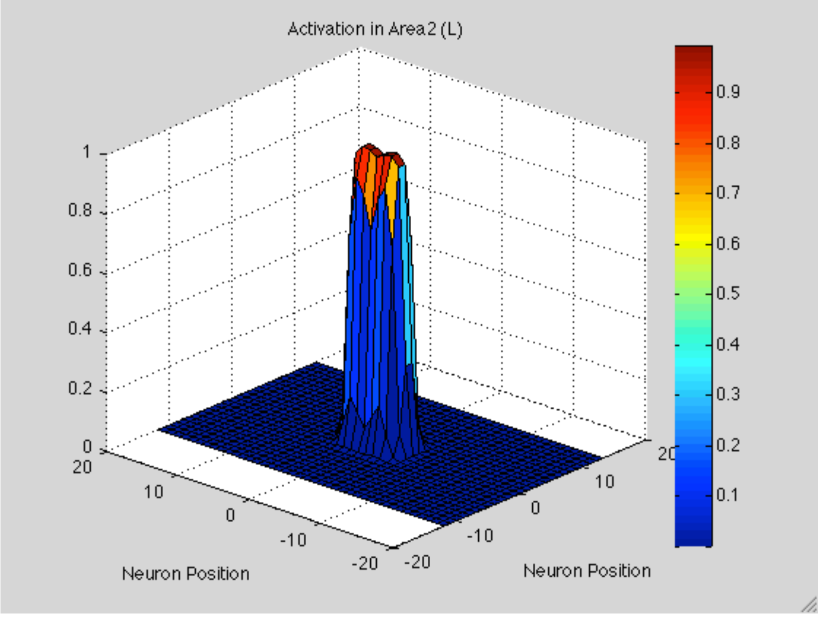


Figure 10.d. 3D representation of Figure 10.c. Only one peak of activation is provided.

So, the neuronal network provides two balls of activation in both Area1 and Area2 by investigating across the dorsum. Within Area2 balls are less discriminable.

Instead, investigating along the dorsum, the model provides a big ball of activation in each Area.

These differences in term of higher-level layer outputs are due to feed-forward synapses from the first layer to the second one. In particular, the oval-shape of these synapses provides a greater excitation across the cortical area (horizontal direction of the matrix) than along the cortical area (vertical orientation of the matrix). Moreover, this effect is increased thanks to lateral synapses within the higher-level layer.

Longitudinal two-point discrimination threshold: 1.2 cm.

Applying two stimuli spaced by 1.2 cm across the dorsum, the model response is the same obtained in the previous case. This means, that distance is coded by 3 neurons both in the first and the second layer.

I cannot say the same as regard the longitudinal orientation. In fact, the model provides a big ball of activation within Area1 whether two different balls can be discriminated in the second layer. This interesting outcome is due to rescaling effect the neuronal network simulates. So, while 1.2 cm is coded by 0 neurons in the first layer, a perceived distance represented by 2 neurons is observed within the higher-level layer.

The figures reported below give us an illustrative explanation.

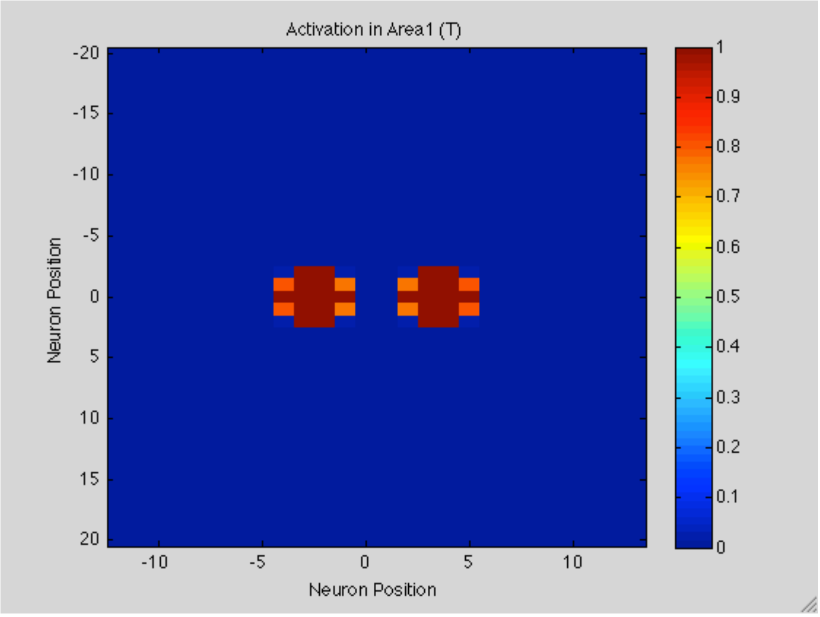


Figure 11.a. 3 neurons encoded for 1.2 cm across the hand.

Applied Distance = 1.2 cm.

*Perceived Distance = **3** Neurons.*

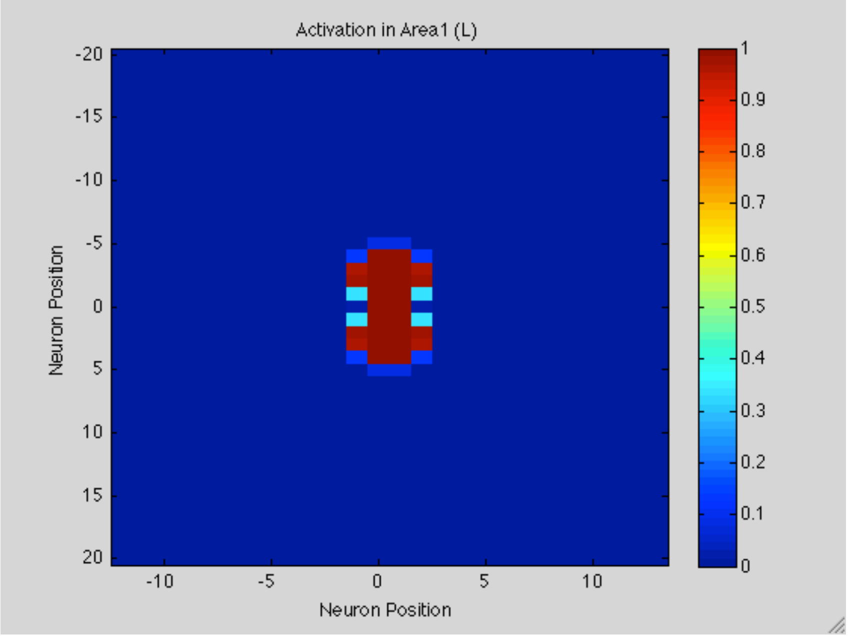


Figure 11.b. **Stimuli along the hand are not discriminated from each other within Area1 if the distance between them is 1.2 cm.**

Applied Distance = 1.2 cm.

Perceived Distance = ***0*** *Neurons.*

Note that Area1 cannot discriminate two stimuli running along the dorsum of the hand for that specific distance.

Different results are presented in Area2.

Taking a look at Figure 11.c (showing response in Area 2 for an across stimulation) it easy to note that the two balls of activation are much more remarkable than those showed in Figure 10.a

In fact, neurons that represent the perceived distance, have got activation values within the range 0.75÷0.78.

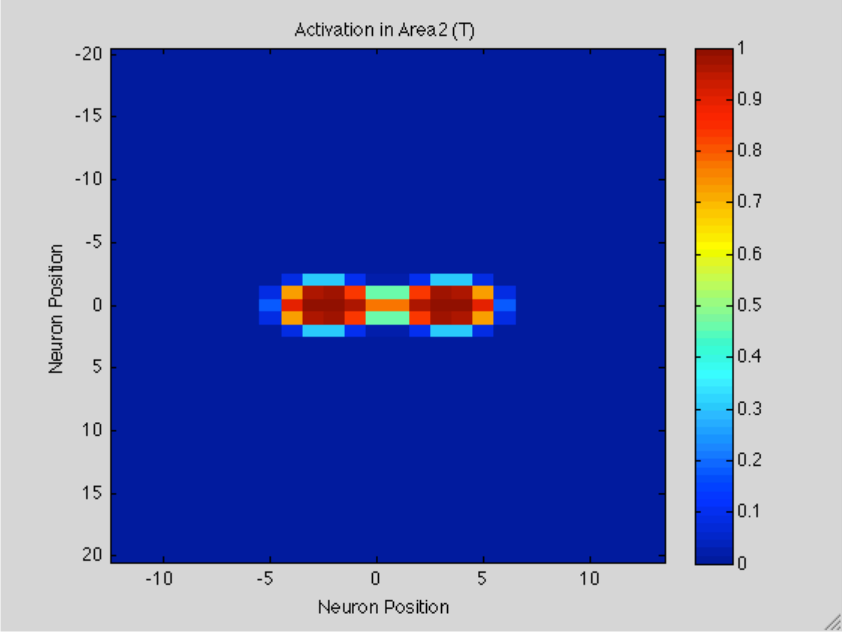


Figure 11.c. As for 1 cm distance, stimuli running across the hand are discriminable from each other.

Applied Distance = 1.2 cm.

*Perceived Distance = **3** Neurons.*

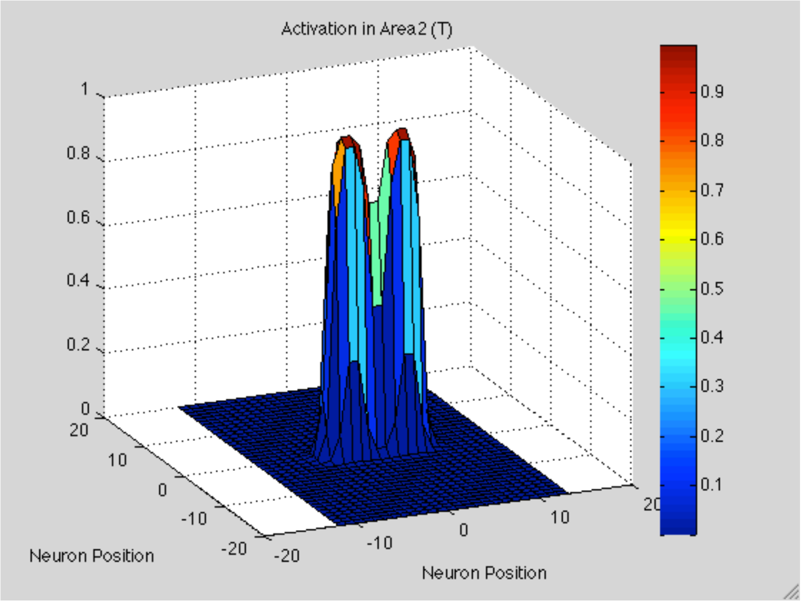


Figure 11.d. 3D view of the previous picture. Peak of activation are discriminated.

The figure above shows a better discrimination of the two peaks. Moreover, considering stimuli running along the dorsum of the hand, the pattern of activation in Area2 is completely different from the one in the first layer. In particular, feed-forward synapses and lateral synapses within Area2 have provided a lower activation along the longitudinal direction. Stimuli are now more discriminable.

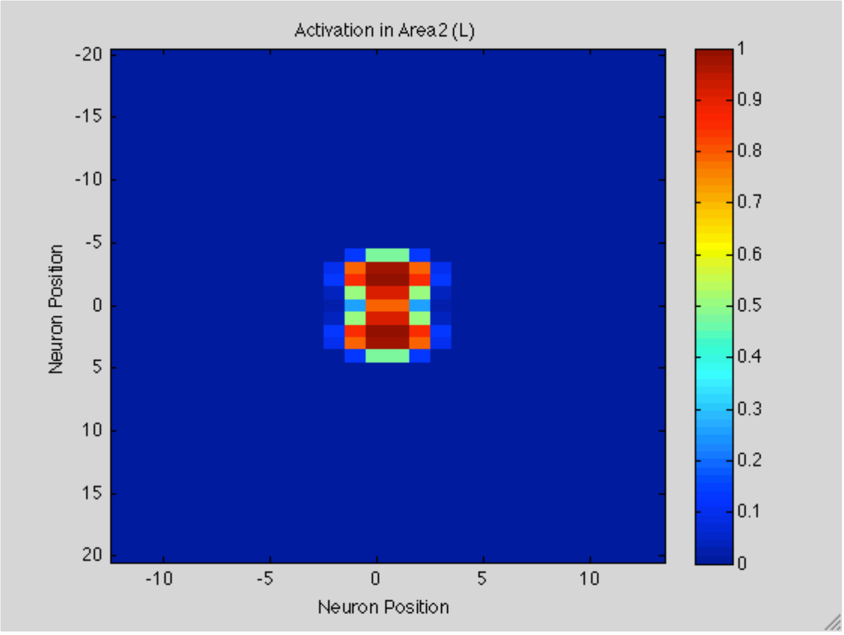


Figure 11.e. 1.2 cm along the dorsum of hand represents the minimal detectable distance within Area2. Bubbles of activation are spaced by 2 neurons.

Applied Distance = 1.2 cm.

*Perceived Distance = **2** Neurons.*

The activation value of the two neurons representing the perceived distance is within the range 0.75÷0.78.

Figure 11.f is a 3D representation of Figure 11.e.

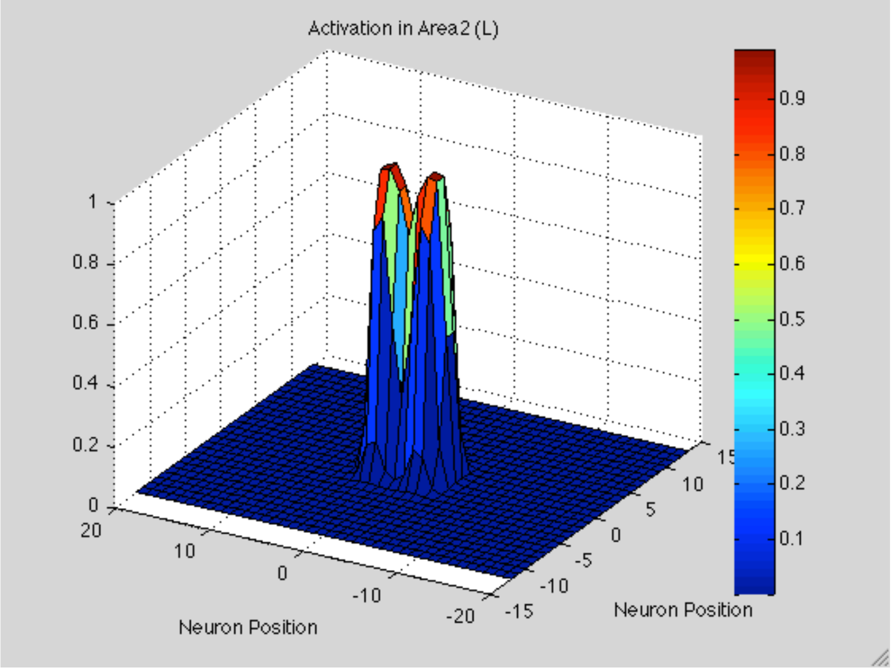


Figure 11.f. A 3D view of the previous picture.

Thanks to the figures reported before it is clear to understand that the activation threshold plays an important role as regards the discrimination of tactile stimuli along each investigated orientation. In fact, by having a look at both Figure 10.a and Figure 11.e, we can note bubbles of activation are not clearly discriminable. This means there is not a noticeable gap between them. Anyway, neurons encoding for the perceived distance have an activation value, which is lower than 0.9 but very close to it.

So, a better discrimination of the bubbles of activation is provided if greater applied distances are investigated.

Figure 12.a shows the pattern of activation within Area2 when two stimuli are applied over the skin surface at an across distance equal to 1.3 cm. The two bubbles of activation are much farther apart than those ones showed in Figure 10.a.

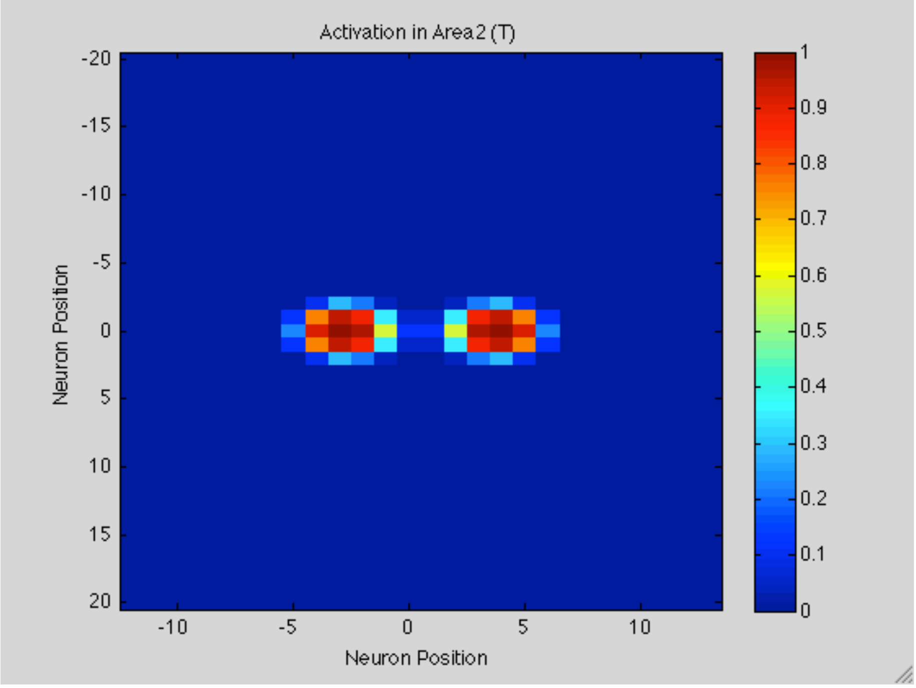


Figure 12.a. Bubbles of activation are clearly discriminable. External stimuli are judged as different and not blurred.

Applied Distance = 1.3 cm.

*Perceived Distance = **5** Neurons.*

Here, the externals stimuli are clearly perceived as different and not blurred. There is a noticeable gap between the bubbles of activation. Neurons encoding for the perceived distance present activation values, which is much lower than the activation threshold.

Figure 12.b clearly demonstrates there is a better discrimination of the bubbles at 1.3 cm than at 1 cm.

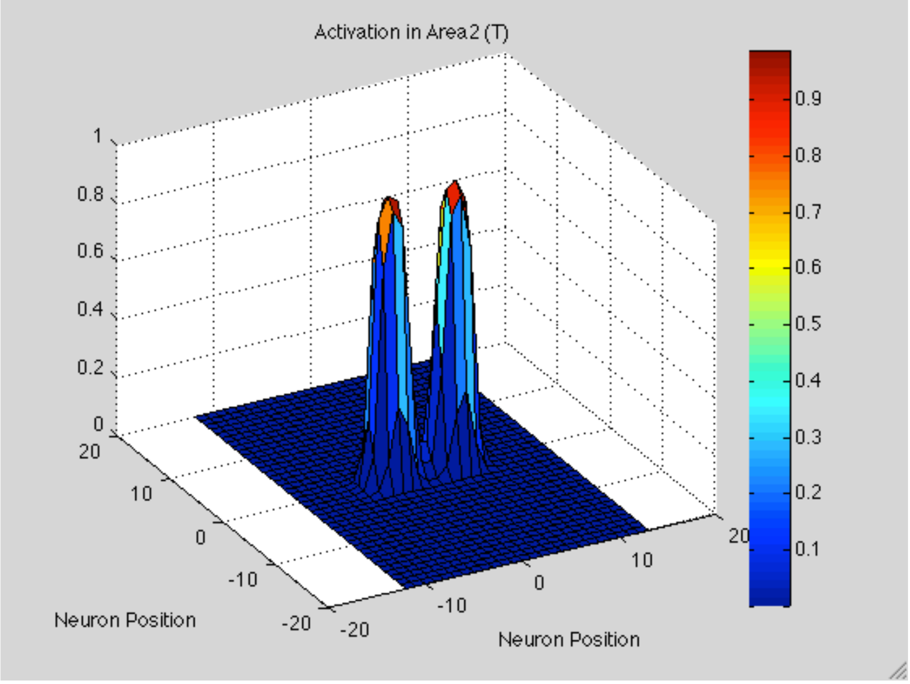


Figure 12.b. 2 different peaks of activation are provided if a distance equal to 1.3 cm is investigated across the hand.

The same considerations are not satisfied along the dorsum of the hand, where two stimuli are judged as only one. Figure 13.a clearly shows what I have just declared. Here we can note there is not such a good discrimination of the bubbles of activation and we can assume there is just one big bubble within Area2.

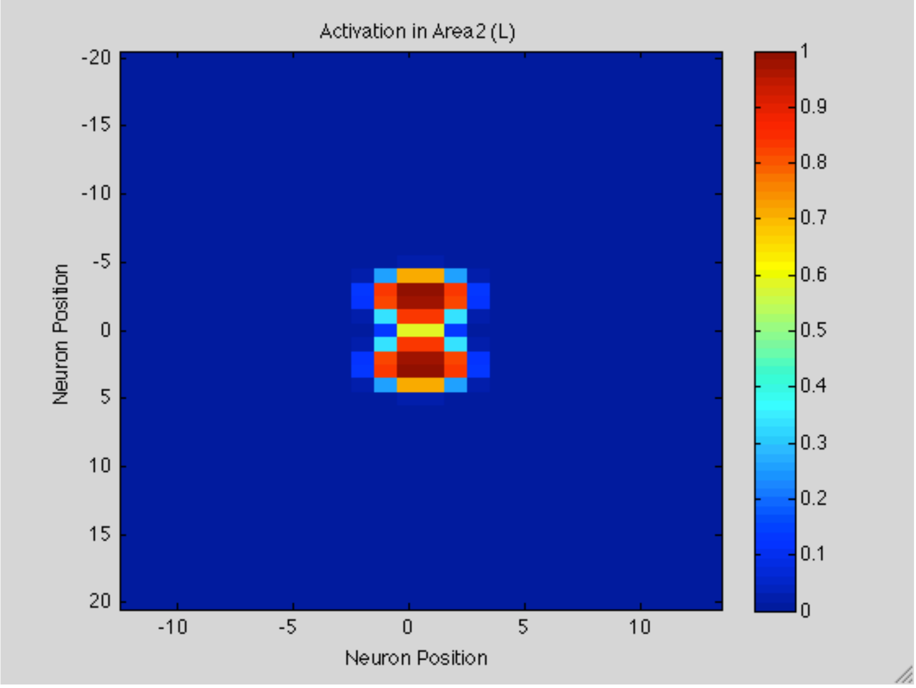


Figure 13.a. External stimuli running along the dorsum of the hand are not judge as different if they are spaced by 1.3 cm.

Applied Distance = 1.3 cm.

Perceived Distance = ***0*** *Neurons.*

By taking a look at Figure 13.b is much easier to understand what I have just written.

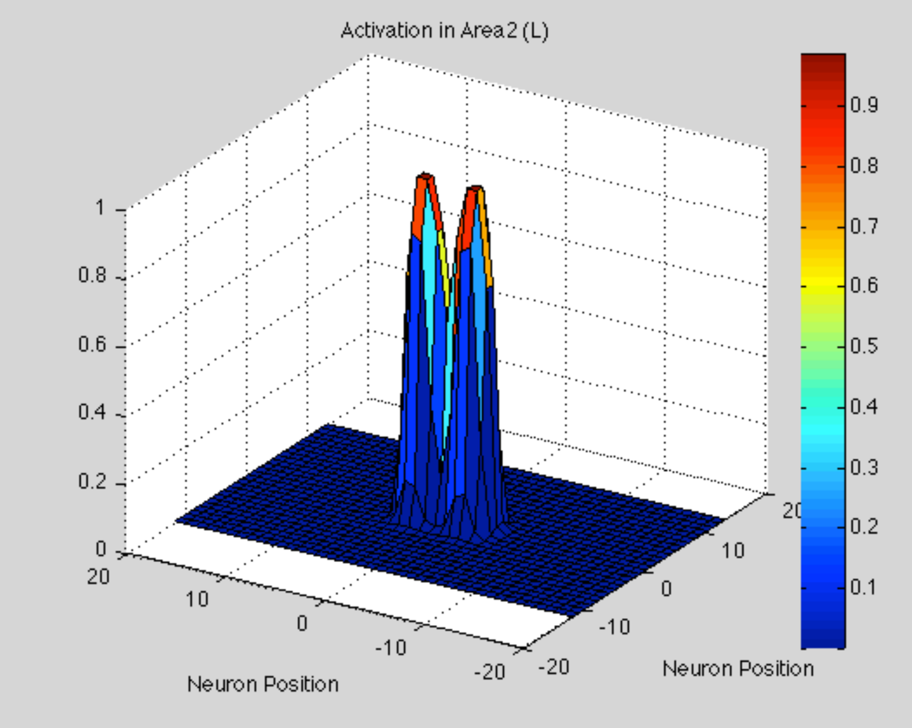


Figure 13.b. Peaks of activation are not well discriminated.

So, two external stimuli applied along the dorsum of the hand can be judged as not only one if they are spaced at a greater distance. In particular, two bubbles of activation represent the pattern of activation within Area2 if stimuli running along the hand are spaced at a distance equal to 1.5 cm.

Obviously, the same consideration is satisfied across the hand. Figure 14.a shows there is a noticeable gap between the bubbles of activation. So, I can say external stimuli are perceived as different. Here, neurons encoded for the perceived distance have activation value that is clearly lower than the activation threshold. As a support, Figure 14.b shows two distinct peaks of activation.

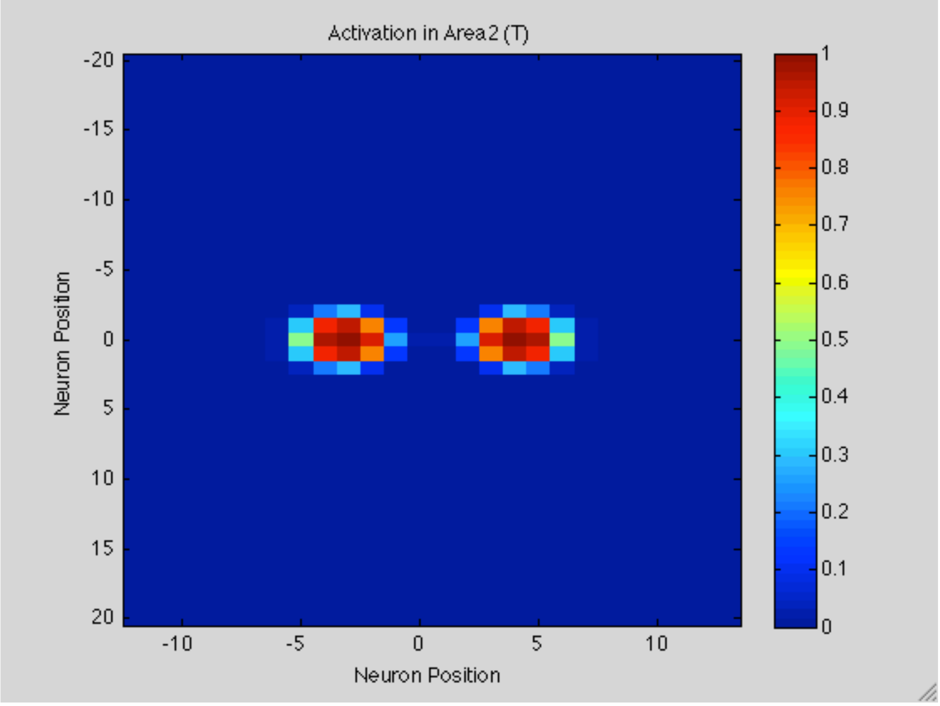


Figure 14.a. Pattern of activation within Area2 if stimuli over the skin are spaced by 1.5 cm.

Applied Distance = 1.5 cm.

Perceived Distance = 5 Neurons.

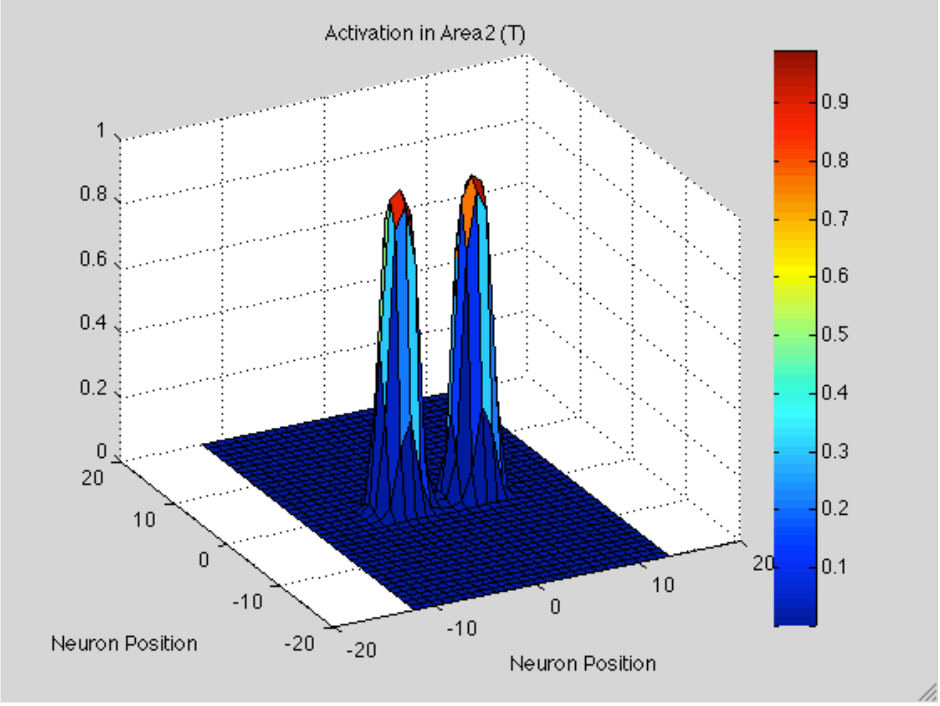


Figure 14.b. A 3d view of the previous picture.

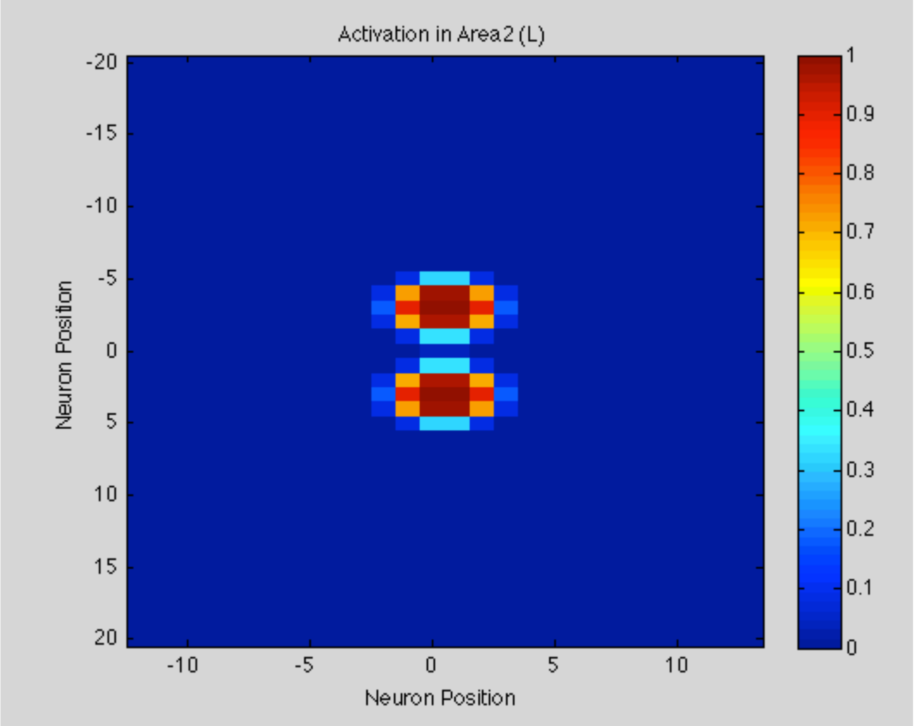


Figure 15.a. 1.5 cm represents the minimal detectable distance along the hand.

Applied Distance = 1.5 cm.

Perceived Distance = 5 Neurons.

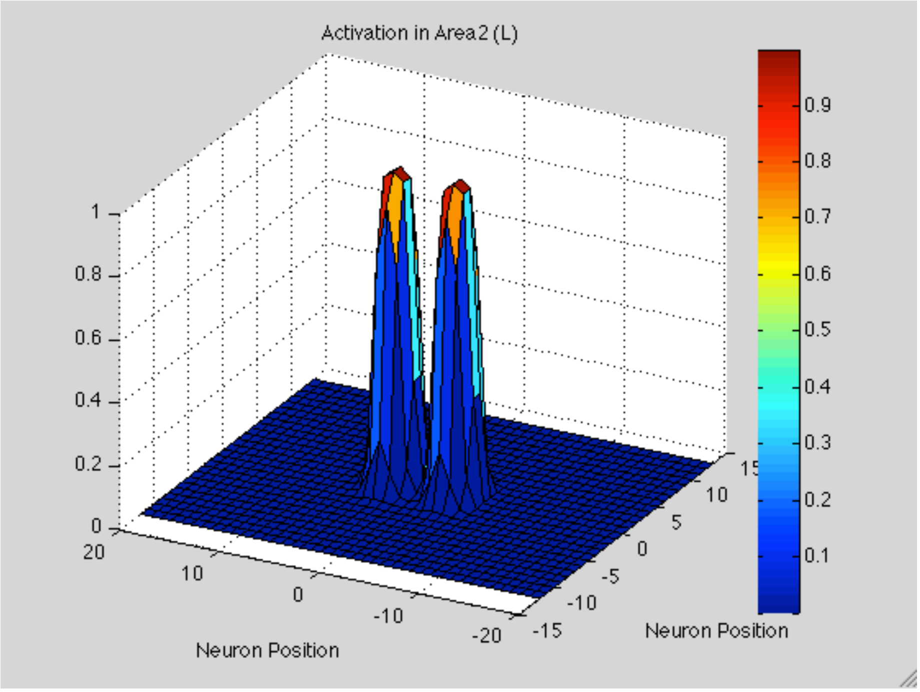


Figure 15.b. Peaks of activation are now well discriminated.

t-Test

By considering each investigated MDV, a simulation composed by 100 trails for each ratio has been conducted.

In order to make statistical comparison, I implemented 10 different simulations, which represent 10 virtual subjects. In this way, independent samples were provided. Any simulation was conducted in the same way with the intent to investigate the 10 different ratios reported before. Outputs from both the first layer and the second layer were computed for each subject. Of course these simulations are very similar to those conducted with 100 tests. For each hypothetical subject, ten trials per ratio were performed, and for each ratio the proportion of across stimuli judged larger than across stimuli was computed.

The tables below show simulations results for both first-level layer and second-level layer by considering a MDV equal to 3 cm and 4 cm respectively.

Table 13

			MDV = 3 cm		
			AREA 1		
Ratios	***Subject 1***	***Subject 2***	***Subject 3***	***Subject 4***	***Subject 5***
0.5	0	0	0	0	0
0.65	0	0	0	0.1	0.2
0.75	0.4	0.2	0.3	0.5	0.3
0.8	0.7	0.5	0.6	0.5	0.3
0.85	0.8	0.8	0.7	0.7	0.6
1	0.9	0.9	0.9	0.9	0.9
1.1	1	1	1	0.9	0.9
1.25	1	1	1	1	1
1.5	1	1	1	1	1
2	1	1	1	1	1

Subject 6	***Subject 7***	***Subject 8***	***Subject 9***	***Subject 10***
0	0	0	0	0
0	0.1	0.1	0	0
0.4	0.5	0.4	0.5	0.7
0.8	0.5	0.5	0.6	0.5

0.8	0.7	0.9	0.9	0.5
1	1	1	1	1
0.9	1	1	0.9	1
1	1	1	1	1
1	1	1	1	1
1	1	1	1	1

Table 15 shows the proportion across stimuli judged larger than along stimuli by each virtual subject. Data are referred to Area1. Each rows indicates the judgment at a specific ratio.

Then PSE, and IQR of each virtual participant were computed. Values are shown in Table 16.

Table 14

Subjects	*PSEs*	*0.25*	*0.75*	*IQRs*
1	0.769	0.719	0.822	0.103
2	0.799	0.760	0.841	0.081
3	0.792	0.731	0.857	0.126
4	0.781	0.688	0.886	0.198
5	0.829	0.729	0.943	0.214
6	0.762	0.720	0.807	0.087
7	0.777	0.699	0.863	0.164
8	0.776	0.722	0.834	0.112
9	0.763	0.713	0.816	0.103
10	0.780	0.691	0.880	0.189

Finally the mean value ($\overline{PSE}$), and standard deviation (σ), and standard error (SE) of the PSE distribution were found.

Respectively:

$$\overline{PSE}_{Area1}^{3cm} = 0.783$$

$$\sigma_{Area1}^{3cm} = 0.020$$

$$SE_{Area1}^{3cm} = 0{,}006$$

SE was computed as:

$$SE = \frac{\sigma}{\sqrt{N}} \tag{3.10}$$

where N indicates the number of subjects that compose the specific population.

Table 17 shows the proportion across stimuli judged larger than along stimuli by each virtual subject. Data are referred to the higher-level layer.

Table 15

			MDV = 3 cm							
			AREA 2							
Ratios	*Subject 1*	*Subject 2*	*Subject 3*	*Subject 4*	*Subject 5*	Subject 6	Subject 7	Subject 8	Subject 9	Subject 10
0.5	0	0	0	0	0	0	0	0	0	0
0.65	0	0	0	0	0	0	0	0	0	0
0.75	0.2	0.1	0.1	0.1	0.1	0.3	0	0.1	0.3	0.1
0.8	0.2	0.5	0.1	0.2	0.1	0.2	0.2	0.1	0.4	0.3
0.85	0.2	0.4	0.3	0.4	0.3	0.5	0.5	0.5	0.6	0.4
1	0.9	0.8	0.8	0.8	0.6	0.9	0.8	0.9	0.5	1
1.1	0.9	0.9	0.9	1	1	0.8	0.8	1	1	0.9
1.25	1	1	1	1	1	1	1	1	1	1
1.5	1	1	1	1	1	1	1	1	1	1
2	1	1	1	1	1	1	1	1	1	1

Each row indicates the judgment at a specific ratio.

Then PSE, and IQR of each virtual participant were compute.

PSE and IQR values are shown in Table 13.

Table 16

Subjects	**PSE**	**0.25**	**0.75**	**IQR**
1	0.899	0.828	0.975	0.147
2	0.864	0.771	0.968	0.197
3	0.910	0.838	0.989	0.151
4	0.884	0.812	0.963	0.152
5	0.931	0.849	1.021	0.172
6	0.863	0.771	0.966	0.195
7	0.891	0.807	0.983	0.176
8	0.861	0.814	0.911	0.097
9	0.859	0.739	0.998	0.260
10	0.859	0.800	0.921	0.120

Finally, as I have done before:

$\overline{PSE}_{Area2}^{3cm} = 0.882$

$\sigma_{Area2}^{3cm} = 0.025$

$SE_{Area2}^{3cm} = 0.008$

It is clear that the same procedure has been used for the 4 cm MDV case.

The following table will report data referred to this specific case.

Table 17

			MDV = 4 cm		
			AREA 1		
Ratios	***Subject 1***	***Subject 2***	***Subject 3***	***Subject 4***	***Subject 5***
0.5	0	0	0	0	0
0.65	0	0.1	0	0	0
0.75	0.4	0.4	0.3	0.4	0.3

0.8	0.4	0.6	0.7	0.4	0.7
0.85	1	0.9	0.9	0.8	0.8
1	0.9	0.9	1	1	0.9
1.1	1	1	1	1	1
1.25	1	1	1	1	1
1.5	1	1	1	1	1
2	1	1	1	1	1

Subject 6	***Subject 7***	***Subject 8***	***Subject 9***	***Subject 10***
0	0	0	0	0
0	0	0	0.1	0.1
0.5	0.2	0.4	0.4	0.3
0.5	0.5	0.7	0.4	0.8
1	1	0.9	0.9	0.7
1	1	1	1	0.9
0.9	1	1	1	1
1	1	1	1	1
1	1	1	1	1
1	1	1	1	1

PSEs and IQRs for each subject are showed in Table 20.

Table 18

Subjects	***PSEs***	***0.25***	***0.75***	***IQR***
1	0.784	0.742	0.829	0.087
2	0.768	0.715	0.826	0.111
3	0.775	0.742	0.810	0.067
4	0.793	0.736	0.855	0.118
5	0.777	0.735	0.823	0.088
6	0.767	0.720	0.817	0.096
7	0.792	0.766	0.821	0.055
8	0.766	0.726	0.809	0.082
9	0.784	0.729	0.844	0.115
10	0.771	0.709	0.838	0.129

Hence:

$\overline{PSE}^{4cm}_{Area1} = 0.778$

$\sigma^{4cm}_{Area1} = 0.010$

$SE^{4cm}_{Area1} = 0.003$

The same has been done for Area2.

Table 19

			MDV = 4 cm							
			AREA2							
Ratios	Subject 1	Subject 2	Subject 3	Subject 4	Subject 5	Subject 6	Subject 7	Subject 8	Subject 9	Subject 10
0.5	0	0	0	0	0	0	0	0	0	0
0.65	0	0	0	0	0	0	0	0	0.1	0
0.75	0.1	0.2	0.2	0.1	0.3	0	0.1	0	0.1	0.2
0.8	0.1	0.1	0.3	0.1	0.3	0.2	0.2	0.2	0.3	0.1
0.85	0.8	0.2	0.6	0.6	0.6	0.5	0.6	0.6	0.5	0.5
1	1	0.9	0.8	0.9	0.9	1	0.9	0.9	0.9	0.9
1.1	1	1	1	1	1	1	0.9	1	1	1
1.25	1	1	1	1	1	1	1	1	1	1
1.5	1	1	1	1	1	1	1	1	1	1
2	1	1	1	1	1	1	1	1	1	1

PSEs and IQRs for each subject are showed in Table 22.

Table 20

Subjects	PSEs	0.25	0.75	IQRs
1	0.830	0.812	0.846	0.0320
2	0.902	0.849	0.960	0.110
3	0.846	0.767	0.932	0.165
4	0.841	0.819	0.865	0.046
5	0.832	0.758	0.912	0.154

6	0.849	0.812	0.888	0.075
7	0.840	0.800	0.880	0.080
8	0.838	0.808	0.870	0.061
9	0.853	0.788	0.923	0.135
10	0.865	0.805	0.929	0.125

Finally:

$\overline{PSE}^{4cm}_{Area2} = 0.850$

$\sigma^{4cm}_{Area2} = 0.021$

$SE^{4cm}_{Area2} = 0.007$

$\overline{PSE}$, and σ, and SE are required in order to perform the Student's test.

It is important to say that data reported either in Table 11 and Table 13 came from the same subjects as well as data reported in both Table 15 and Table 17. So, in order to assess if $\overline{PSE}^{3cm}_{Area1}$, and $\overline{PSE}^{3cm}_{Area2}$, and $\overline{PSE}^{4cm}_{Area1}$, and $\overline{PSE}^{4cm}_{Area2}$, respectively, are statically different from each other, *Paired t-Test* has been performed.

I could not use Two-Sample t-Test because participants have been tested twice. In particular the ten virtual subjects were tested prior as to Area1 and then tested again as to Area2. So, by performing Paired t-Test, I can investigate mean values of two different data distribution coming from the same participants.

Conversely, *One-Sample t-Test* was used to compare statistically results of section 5 in order to verify if each $\overline{PSE}$ was statistically related to that one found by Longo & Haggard.

In this kind of t-Test, the mean value of a distribution is compare to a constant value.

Instead, results in Section 3 and Section 4 have been investigated thanks to Two-Sample t-Test. In fact, these two cases report data distribution coming from two different subject populations. That is, Subjects tested to a MDV equal to 3 cm differ to those tested to a MDV equal to 4 cm.

t-Test were performed using two different Matlab R2009b function (t-test and t-test2).

In particular, H0=0 indicates that the null-hypothesis can be rejected at the 5% significance level whether H0=1 indicates that the null-hypothesis cannot be rejected at the 5% level.

t-Test: case study 1.

Considering the Case of study 1, Paired t-Test was performed in order to assess if $\overline{PSE}_{Area1}^{3cm}$, and $\overline{PSE}_{Area2}^{3cm}$ were statistically related.

If the two data distributions (PSEs of Area1 and PSE of Area2 respectively) are the same, it will be impossible to discriminate $\overline{PSE}_{Area1}^{3cm}$ from $\overline{PSE}_{Area2}^{3cm}$ statistically.

- Hence the null-hypothesis is H0: “The two PSE distribution mean values are equal to each other”.

In order to found if the null-hypothesis could be rejected the *t* value was computed by using the formula below:

$$t(df) = \frac{\frac{\sum D}{N}}{\sqrt{\frac{\sum D^2 - \frac{(\sum D)^2}{N}}{N \cdot (N-1)}}} \qquad \textbf{(3.12)}$$

where *df* short for degrees of freedom. D is the difference between the PSE values referred to Area1 and Area2 of the same subject. N is the number of participant, which is equal to 10.

t(9) = −16.17 → p = 5.88e-08 → p < .0001 → H0 = 0

The null-hypothesis can be clearly rejected. In fact, the probability the two means of the investigated distribution could be the same, is less than .0001.

Moreover, since the ideal case (no tactile illusion: *PSE*=1) has been compared with the data distribution within Area1 as well as that referred to Area2, the respective t-Test values are reported below:

$\boldsymbol{t_{Area\,1}^{ideal\,case}(9) = -34.28}$ → ***p = 7.54e-11*** → ***p < .0001*** → ***H0 = 0***

$\boldsymbol{t_{Area\,2}^{ideal\,case}(9) = -14.71}$ → ***p = 1.34e-07*** → ***p < .0001*** → ***H0 = 0***

In particular:

- H0: "The mean values ($\overline{PSE}$) of the two investigated groups are equal to 1".

Once again the null-hypothesis can be rejected.

Note that $\overline{PSE}_{Area1}^{3cm}$, and $\overline{PSE}_{Area2}^{3cm}$ have been compared with constant value. This is why the formula performs the two previous t-Test values is referred to One-Sample t-Test.

In general:

$$t_{Area\ 1}^{ideal\ case} = \frac{\overline{PSE_{Area1}^{3\ cm}}-1}{SE_{Area1}^{3\ cm}} \qquad \textbf{(3.13)}$$

Equation 3.13 is referred to the mean PSEs value within Area1. The same formula has been implemented for Area2. Obviously, the subscript Area1 should be replace with Area2.

t-Test: case of study 2.

In this case of study, the t-Test was performed following the same main steps of the case before.

So, the null-hypothesis is the same of the previous case.

Moreover, the t-Test values were computed by using equation 3.12 as well as equation 3.13. Note that in this case, the superscript 3 cm in both the equation should be replaced with 4 cm.

Any t-Test value is reported below.

t(9) = – 8.30 → p = 1.65e-05 → p < .0001 → H0 = 0

$t^{ideal\,case}_{Area\,1}(9) = -68.96$ → ***p = 1.43e-13 → p < .0001 → H0 = 0***

$t^{ideal\,case}_{Area\,2}(9) = -22.34$ → ***p = 3.42e-09 → p < .0001 → H0 = 0***

Once again the t-Test indicates that the investigated mean values and the constant are statistically different from each other.

t-Test: case of study 3.

Here, the two investigated groups are represented by the PSEs of subjects referred to Area1 in cases of 3 cm MDV and 4 cm MDV. Student's Two-Sample t-Test has been performed using *ttest2*, which is a function of Matlab R2009b.

The null-hypothesis considerate at this specific case of study is the following:

- H0: "The mean values ($\overline{PSE}$) of the two investigated groups are equal to each other".

So, the t-Test value is compute thanks to the formula below.

$$t(df) = \frac{\overline{PSE^{3cm}_{Area1}} - \overline{PSE^{4cm}_{Area1}}}{\sqrt{SE^{3cm}_{Area1} + SE^{4cm}_{Area1}}} \qquad \textbf{(3.14)}$$

Since the two PSE distributions are very similar, $\overline{PSE}^{3cm}_{Area1}$, and $\overline{PSE}^{4cm}_{Area1}$ presents values, which are close to each other.

As I wrote before, taking a look at Figure 5 we can note that the two groups are about the same (curves are overlapping).

t-Test confirmed this relationship.

t(18) = 0.67 → p = 5.10e-01 → p > .05 → H0 = 1

In this case of study, p > 0.05, that is, the set of data failed to rejected the null-hypothesis. So, the two investigated distribution are not statistically different from each other. This is what I expected since the two curves are almost overlapped.

t-Test: case of study 4.

The following case of study differs from the previous one only in term of investigated cortical area. As before, the comparison was made between PSEs in case of 3 cm MDV and 4 cm, with reference to Area 2. t-Test was performed according to the same main steps seen before.

Results indicate that the means of the two distributions statistically different. In fact, the probability referred to this event is clearly lower than 0.05. In other words, the null-hypothesis can be rejected.

t(18) = -3.1 → p = 6.20e03 → p < .001 → H0 = 0

Chapter 4

Parameter Sensitivity Analysis

In this chapter I am going to report the Sensitivity Analysis I have conducted in order to investigate the robustness of the statistical neuronal network, with respect to parameter values. In particular I focused on certain parameters that played a key role during the simulation.

As the perceived distance is represented by the output from the higher-level layer, I investigated the behaviour of the model by changing parameter values related to feed-forward synapses as well as lateral ones within the second level layer. In this way, seven different parameters have been perturbed.

The distances I have considered in order to provide the investigated ratios (Across/Along), are those referred to the 4 cm MDV case.

Moreover, 25 trials at each ratio have been executed.

Any conducted test is reported below.

Lateral Synapses within Area2

The first six cases describe the neuronal network behaviour and its results by perturbing parameters associated to the lateral synapses within the higher-level layer.

The other cases are referred to the feed-forward synapses.

Case 1: Decreasing Lateral Synapses' dimensions.

As described in Chapter 2, lateral synapses in the higher-level layer, have got a Mexican hat shape. So, by decreasing of a factor equal to 1 the standard deviation referred to both the excitatory and

inhibitory Gaussian functions, lateral synapses decrease in their dimensions. This means, one neuron can excite or inhibit fewer neurons within the layer simulated by the neuronal network.
In particular:

$$\sigma_{ex}^{Area2} = 1.40\, neurons \rightarrow 0.40\, neurons$$

$$\sigma_{in}^{Area2} = 1.75\, neurons \rightarrow 0.75\, neurons$$

$$\frac{\sigma_{in}^{Area2}}{\sigma_{ex}^{Area2}} = 1.25 \rightarrow 1.88$$

Note that by decreasing standard deviations, the ratio between them becomes higher.
The intensity of the excitatory and inhibitory Gaussian functions has not been perturbed.
According to these modifications, pattern of lateral synapses within Area2 appears as shown in Figure 1.

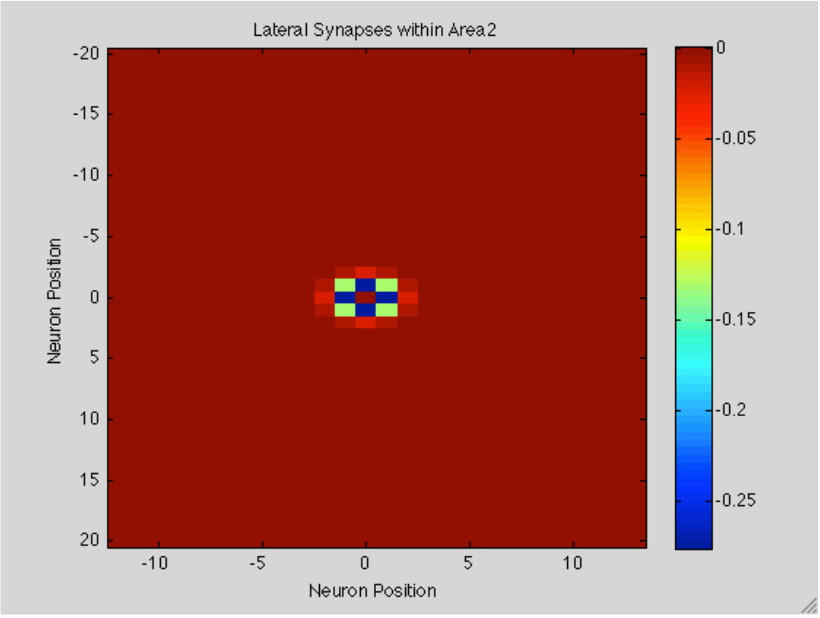


Figure 1. Note that by decreasing lateral synapses dimension excitatory effects are not provided.

The previous picture clearly demonstrates that as the excitatory Gaussian function is very narrow, the resulting lateral synapses provide only inhibitory effects.

By using this pattern of lateral synapses in Area 2, the resulting outcomes from Area1 and Area2 are represented by the two Gaussian Cumulative curves visualized in Figure 2.

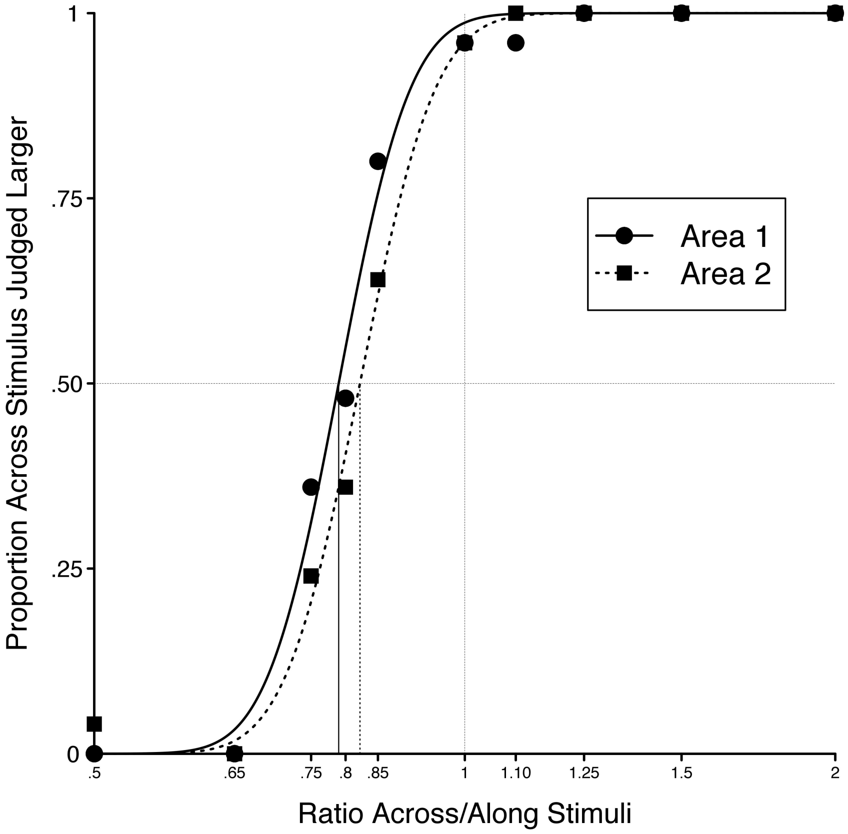


Figure 2. **The settings reported above provide a $\text{PSE}_{\text{Area2}}$ a bit lower than that one provided by settings reported in Chapter 2. Anyway, there is not a discriminable difference as bubbles of activation shrink in both the investigated orientations and not just along only one of them.**

It easy to note that rescaling effect as well as orientation-dependent tactile illusion was still provided with the settings seen before. Hence:

Table 1

$\text{PSE}_{\text{Area1}}$	$\text{PSE}_{\text{Area2}}$	Rescaling Effect Magnitude	Orientation-Dependent Tactile Illusion Magnitude
0.790	0.822	0.032	0.178

In particular, PSE_{Area2} was lower than the value computed by the model using the settings reported in Chapter 2 ($PSE_{Area2} = 0.851$).

So, by comparing PSEs referred to Area2, I can say there is not a discriminable difference between them. This result was completely expected. In fact, by decreasing the size of the lateral synapses, balls of activation shrank in both the investigated orientations and not just along only one of them.

Moreover, Case 1 did not reflect the assumption I have made about rescaling process. The adopted solution in order to provide rescaling consists in changing perceived distance value along the orientation with less spatial resolution and less sensory acuity too. In fact, it is licit to think that nothing should change from Area1 to Area2 (in term of perceived distance) if transversal stimuli are applied because of both better spatial resolution and sensory acuity. In other words, it seems ecologically more beneficial to improve the functionality where it is poorer (that is along the orientation showing lower resolution) and to preserve it where it is higher (that is along the orientation showing better resolution).

In order to assess what I said before, two factors were computed and reported in the table below.

Here, the factor related to the along case was similar to that one reported in the previous chapter but this does not hold for the transversal orientation.

In fact:

	Across	**Along**
% Changing	100%	100%
Mean Changing Value (Neurons)	-2.27	-2.71

That is, the rate of trials showing differences in term of perceived distance between Area1 and Area2 (%C) was equal to the 100% at any investigated orientations. In particular, the Mean Changing Value (indicating the mean value of the differences between perceived distance in Area1 and Area2) was -2.27 neurons across the hand and -2.71 along the hand.

So, the assumption made about rescaling was not verified. In fact, at any ratio, distances across the hand were not preserved. That is, from Area1 to Area2, distances became larger. In particular each distance is augmented by more than 2 neurons.

So, by decreasing lateral synapses' dimensions rescaling assumption was not satisfied.

Case 2: Increasing Lateral Synapses' dimensions.

By increasing the standard deviation, of a factor equal to 1, referred to both the excitatory and inhibitory Gaussian functions, the lateral synapses increased in their dimensions. This means, one neuron could excite or inhibit more neurons within the layer simulated by the neuronal network.

In particular:

$$\sigma_{ex}^{Area2} = 1.4\, neurons \rightarrow 2.4\, neurons$$

$$\sigma_{in}^{Area2} = 1.75\, neurons \rightarrow 2.75\, neurons$$

$$\frac{\sigma_{in}^{Area2}}{\sigma_{ex}^{Area2}} = 1.25 \rightarrow 1.15$$

Note that by decreasing standard deviations, the ratio between them becomes lower.

As in Case 1, the intensity of the excitatory and inhibitory Gaussian functions preserves their values.

As a consequence of these parameter changes, the pattern of lateral synapses within Area 2 modifies as shown in Figure 3.

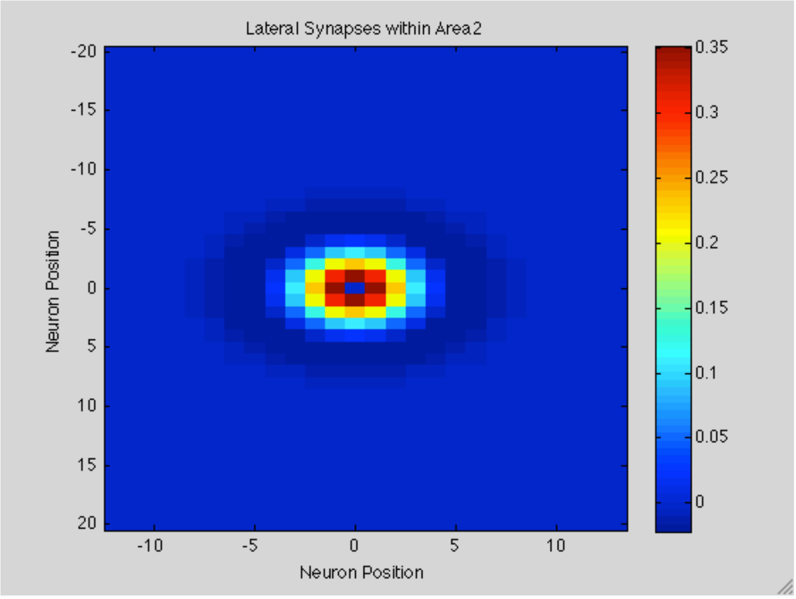


Figure 3. By increasing the lateral synapses' dimension excitatory effects are much more remarkable.

In this case, lateral synapses exert a stronger and wider excitation with respect to basal parameter values.

Figure 4 gives an illustrative view of the final outputs provided by the model.

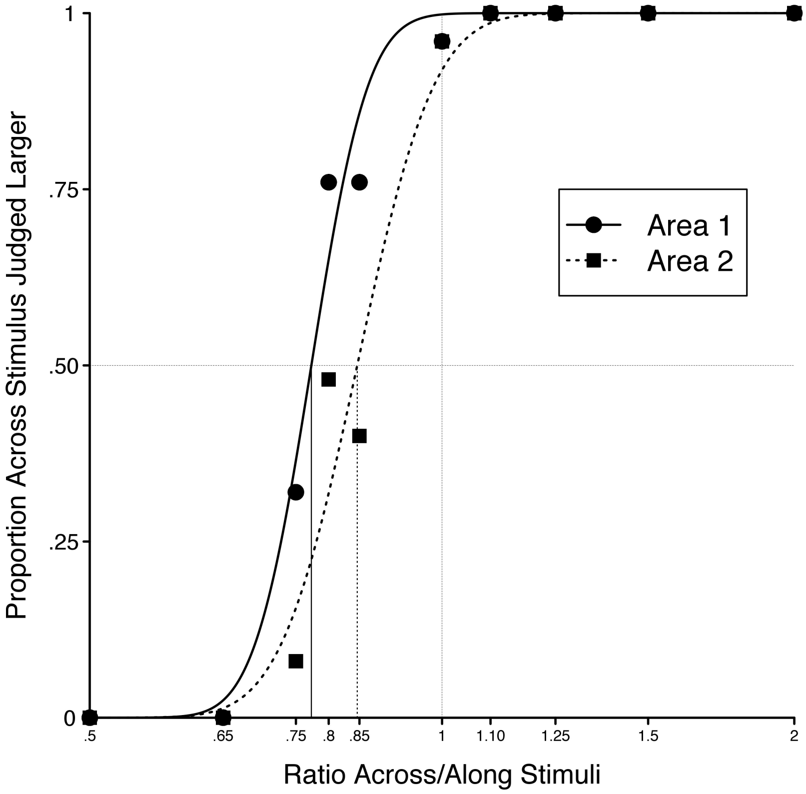


Figure 4. Final results referred to Area1 as well as Area2. No differences in term of PSE$_{Area2}$ were found. It presents the same value of PSE$_{Area2}$ reported in Chapter 3.

In particular:

Table 2

PSE$_{Area1}$	PSE$_{Area2}$	Rescaling Effect Magnitude	Orientation-Dependent Tactile Illusion Magnitude
0.773	0.846	0.073	0.154

Note that this particular case provided final results (see Table 2), which are very similar to those shown in Table 10 of Chapter 3 (data referred to 4 cm MDV). So, by increasing lateral synapses' dimension there were no differences in term of outcomes. In particular, rescaling effect magnitude is the same.

In addition, the assumption about rescaling was satisfied (see the table below).

	Across	Along
% Changing	18%	91%
Mean Changing Value (Neurons)	-1	-1.51

Focusing on the longitudinal orientation, balls of activation within the second layer were still smaller compared to those present in the first layer. However they were bigger than those simulated by the model using parameter settings reported in Chapter 2. In fact, in this case, the perceived distance increased of 1.51 neurons whereas in Case of study 2 (Chapter 3), the MCV was equal to 2.57 neurons.

Moreover, not at every trial perceived distance changes from lower-level layer to higher-level layer. In some trials, the perceived distance was preserved.

Different conclusion can be drawn for the transversal orientation. Here, the % Changing was clearly less than 36% (reported in Chapter 3), indicating that only few trials presented differences in term of perceived distance between Area1 and Area2. The MCV was 1 demonstrating that perceived distance within Area2 differs no more than 1 neuron with respect to Area1.

A disadvantage of this configuration is that – although the along %C was close to the 100% - a MCV equal to 1.51 is similar to the value of MCV in the transversal orientation (= 1),

Another disadvantage of this lateral synapses configuration is related to the two-point discrimination threshold.

There was not difference between transversal and longitudinal orientation as regards the minimal distance that could be perceived.

In fact, two-point discrimination threshold was equal to 1.5 cm in both the investigated orientations. Even if the 1.5 cm distance across the hand was not judged as equal as along the hand (5 neurons across the hand and 4 neurons along the hand), I deem this result not satisfactory since a different 2PDT should be expected.

Case 3: Increasing the inhibitory Gaussian function's standard deviation.

By increasing the standard deviation referred to the inhibitory Gaussian function, of a factor equal to 0.5, only few neurons receive noticeable excitatory effect. As a consequence, it was expected that bubbles of activation within the second layer were smaller than those within the first layer.

In particular:

$$\sigma_{ex}^{Area2} = 1.4\, neurons$$

$$\sigma_{in}^{Area2} = 1.75\, neurons \rightarrow 2.25\, neurons$$

$$\frac{\sigma_{in}^{Area2}}{\sigma_{ex}^{Area2}} = 1.25 \rightarrow 1.96$$

The settings reported above provided a pattern of lateral synapses that it is reported in the figure below.

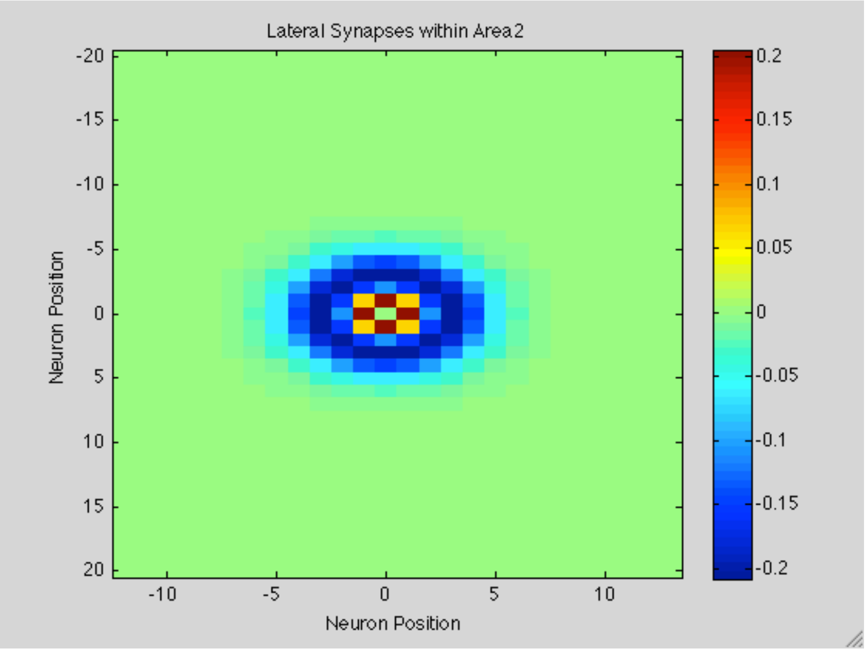


Figure 5. By increasing the inhibitory standard deviation inhibitory effect predominates on the excitatory one.

The model outcomes obtained by using synapses in Figure 5 are reported in the following table.

Table 3

PSE_{Area1}	PSE_{Area2}	Rescaling Effect Magnitude	Orientation-Dependent Tactile Illusion Magnitude
0.773	0.781	0.008	0.219

The table clearly shows interesting results. In fact, PSE_{Area2} strongly differ from 0.85 and it is more similar to the PSE value found by Longo as regards the dorsum of the hand. This suggests that, with this set of parameters, the model could better simulate orientation-dependent tactile illusion over this specific body region.

Note that, the magnitude of rescaling is very low.

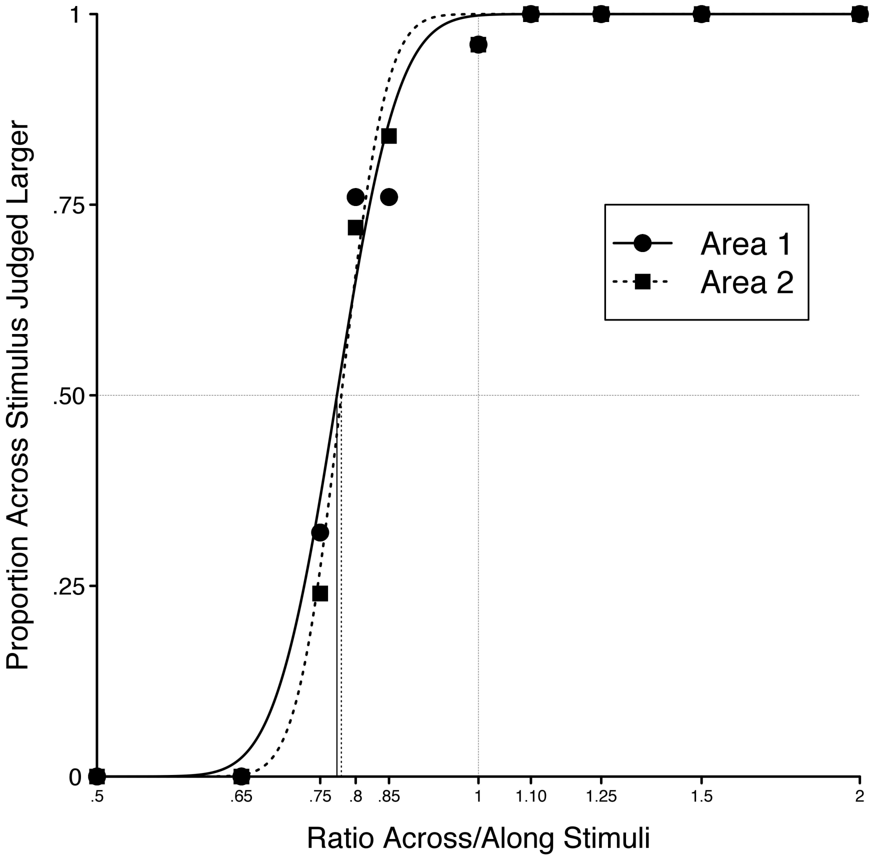


Figure 6. By increasing the inhibition, the neuronal network provided a PSE value within Area2, which is close to that one found over the dorsum of the hand.

The small entity of rescaling emerges also by considering at %C as well as MCV at the two orientations.

	Across	Along
% Changing	100%	100%
Mean Changing Value (Neurons)	-1.58	-2.05

In particular, in this case, the separation between the two bubbles of activations increases – when shifting from Area 1 to Area 2 – in both directions, with higher effects on the longitudinal direction.
The settings provided a two-point discrimination threshold equal to 1.3 cm along the transversal orientation whereas it was equal to 1.5 cm along the opposite direction.

Case 4: Increasing the excitatory Gaussian function's intensity.

In this case I investigated how lateral synapses' intensity could affect outcomes from the second layer. To this aim, the intensity of the Gaussian excitatory function was increased.
That is:

$$L_{ex} = 1.2 \rightarrow 2.2$$

$$L_{in} = 0.8$$

$$\frac{L_{ex}}{L_{in}} = 1.5 \rightarrow 2.75$$

The intensity of the inhibitory Gaussian function was maintained unaltered, as well as the values of the standard deviations. Lateral synapses resulting from this change are shown in Figure 7.

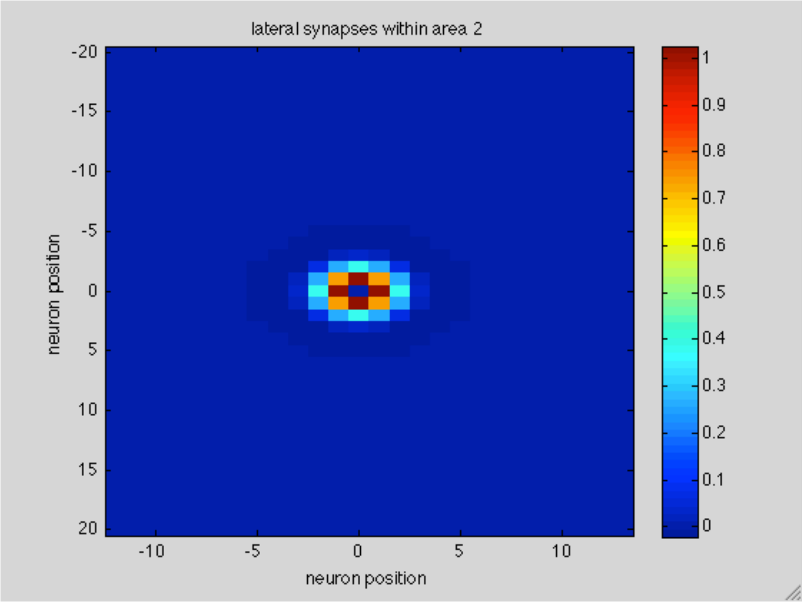


Figure 7. Pattern of lateral synapses within Area2.

The model output from Area1 and Area2 are shown in Figure 8. Note that there is only small difference with respect to results obtained with basal parameter values (see Chapter 2). In fact, PSE_{Area2} is about the same.

The rescaling effect is significantly reduced with respect to basal parameter values (rescaling effect magnitude = 0.073)

The table below shows the final outputs.

Table 4

PSE_{Area1}	PSE_{Area2}	Rescaling Effect Magnitude	Orientation-Dependent Tactile Illusion Magnitude
0.787	0.820	0.033	0.18

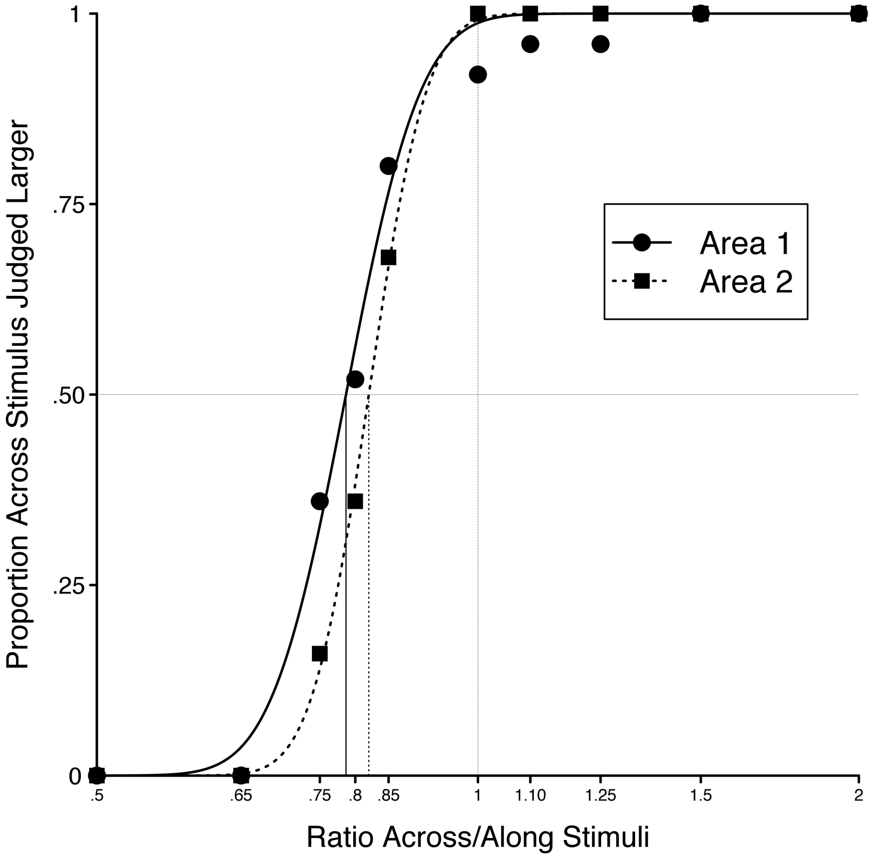


Figure 8 Neuronal network outcomes are similar to those obtained with the basal parameter values.

Indeed, *increasing lateral excitation tends to enlarge the transversal size of the two balls of activation within the higher-level layer. Hence, the number of neurons coding the perceived distance became smaller. Moreover, an increment of the distance along the longitudinal orientation is not provided, preserving almost the same number of neurons from Area1 to Area2.*

Indeed:

	Across	**Along**
% Changing	100%	39%
Mean Changing Value (Neurons)	1.05	1

Note that at any trial, perceived distance decreased of about 1 neuron across the hand whereas along the hand only the 39% of the trials shown changing in perceived distance. Moreover, MCV is no more than one neuron.

Case 5: Decreasing the excitatory Gaussian function's intensity.

The case is clearly the opposite case of the previous one. Anyway, I did not decrease the excitatory intensity of a factor equal to 1 but only of 0.4. In this way, L_{ex} is equal to L_{in}. Standard deviations preserved their values.
Hence:

$$L_{ex} = 1.2 \rightarrow 0.8$$
$$L_{in} = 0.8$$
$$\frac{L_{ex}}{L_{in}} = 1.5 \rightarrow 1$$

Lateral synapses provide only inhibition as indicated in Figure 9. Obviously, by simply decreasing the excitatory intensity, the final effect was the opposite one found out in Case 3. This means, balls of activation were smaller and more neurons, setting between the centres of them, presented an activation value lower than the activation threshold. So, from Area1 to Area2 perceived distance becomes higher.
Results are not satisfactory since:

	Across	**Along**
% Changing	100%	100%
Mean Changing Value (Neurons)	-1.69	-2.45

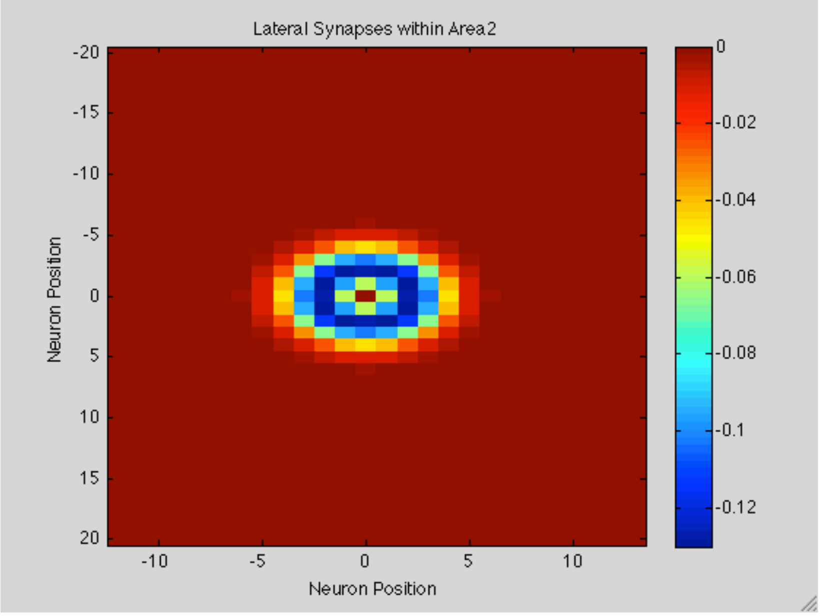


Figure 9. Pattern of lateral synapses of a generic neuron within Area2. The settings provide only inhibitory effects

The two cumulative Gaussian functions (one per layer) are almost superimposed (see Figure 10). *In other words, rescaling effect provided by the feed-forward synapses was counterbalance by the inhibitory effect due to lateral synapses within Area2.*

PSE values, and Rescaling Effect Magnitude as well as Orientation-Dependent Tactile Illusion Magnitude are shown in Table 5.

Table 5

PSE_{Area1}	PSE_{Area2}	Rescaling Effect Magnitude	Orientation-Dependent Tactile Illusion Magnitude
0.792	0.808	0.015	0.192

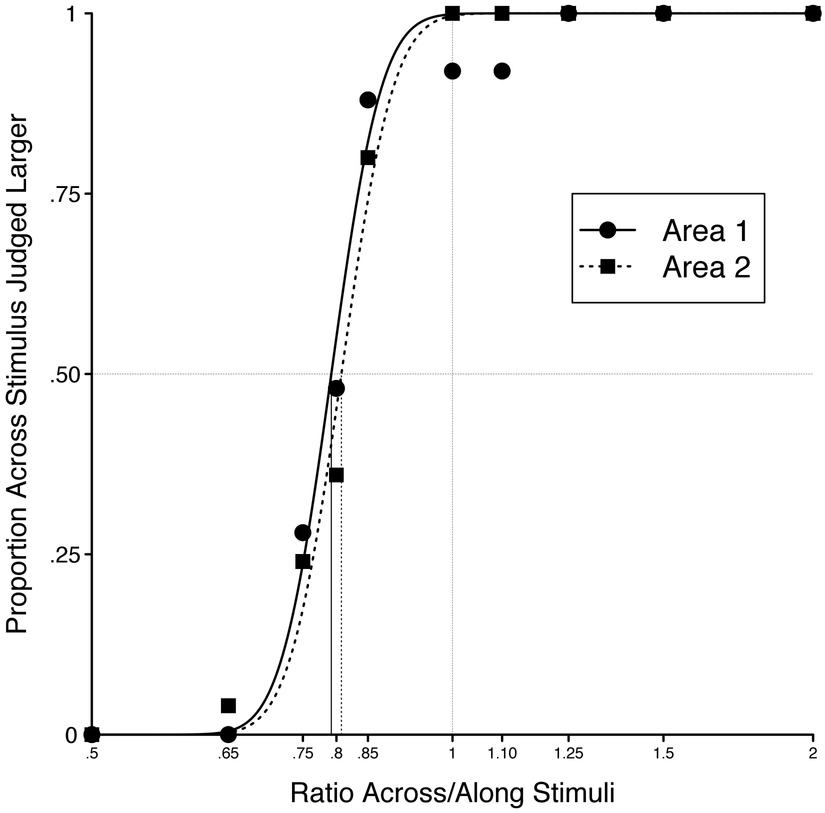


Figure 10. Cumulative Gaussian functions are almost superimposed.

Case 6: Increasing the inhibitory Gaussian function's intensity.

Here, the inhibitory Gaussian function's intensity was reduced by a factor equal to 0.4. In this way L_{in} became equal to L_{ex}.
That is:

$L_{ex} = 1.2$

$L_{in} = 0.8 \rightarrow 1.2$

$\frac{L_{ex}}{L_{in}} = 1.5 \rightarrow 1$

Hence, only inhibition is provided by lateral synapses: this case is similar to case 4.
Indeed, obtained results are:

	Across	Along
% Changing	100%	100%
Mean Changing Value (Neurons)	-1.72	-2.67

That is, there is not significant difference between what happen within Area1 and Area2. That is, as in the previous case, the two curves were very close to each other.

Case 7: No inhibitory effect.

In this case the inhibitory effect of lateral synapses was completely eliminated. That is, L_{in} is set equal to 0 in order to test the response of the neuronal network by only simulating excitatory effect in the higher-level layer.

By focusing on the behaviour of the computational model I can say that Case 7 is similar to Case 3. In other words, if only excitation was provided, balls of activation within Area2 were bigger than those within Area1. So, as a consequence, inside the second level layer distance between the two activation balls is smaller.

Obviously, these considerations held in both transversal and longitudinal direction.

So:

$L_{ex} = 1.2$

$L_{in} = 0.8 \rightarrow 0$

$\frac{L_{ex}}{L_{in}} = 1.5 \rightarrow /$

The following picture shows the pattern of lateral synapses entering in a generic neuron of the neuronal network.

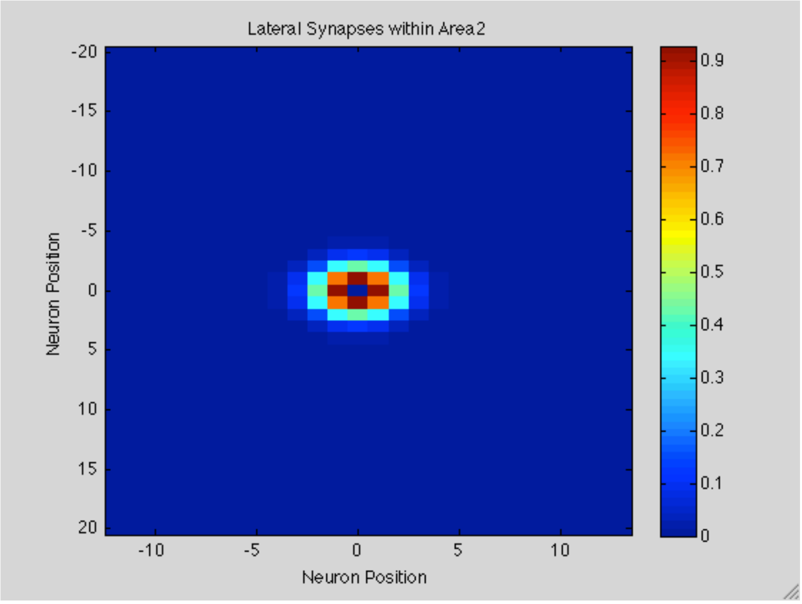


Figure 11. **Pattern of lateral synapses of a generic neuron within Area2. The settings provide only excitation.**

The proportion of across stimulus judged larger was quite different from what reported in Case 3.

Considering the cumulative Gaussian curve representing Area2, we can note there is a greater PSE value. Balls of activation became larger at any investigated orientation. This is not enough to explain why the proportion of across stimuli judged larger is less than 1 in correspondence of ratio greater than 1.. We need to consider that feed-forward synapses play an important rule as regards this aspect. *They provided a greater excitation over the transversal direction. So, within the higher-level layer, perceived distance across the hand decreased by a factor which was greater than the one in the along orientation.*

For that reason, PSE value is greater in this case.

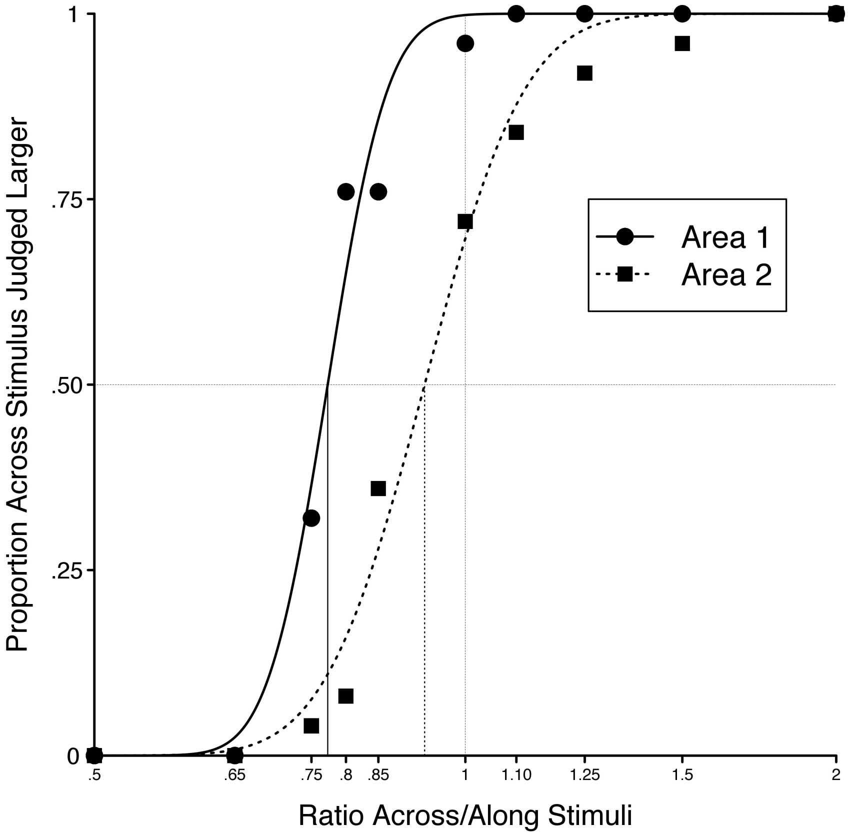


Figure 12. Proportion across stimulus judged larger than longitudinal one by considering any simulated area. Note that PSE_{Area2} is very similar to that one found by Green and Longo as regards the palm.

Figure 12 clearly shows the rescaling effect played an important role. In particular, the magnitude of the rescaling effect was higher than in basal conditions.

Results are shown in the table below.

Table 6

PSE_{Area1}	PSE_{Area2}	Rescaling Effect Magnitude	Orientation-Dependent Tactile Illusion Magnitude
0.773	0.927	0.154	0.073

So, by removing inhibitory effect there were more trials that gave a negative response (along stimulus judged larger).

	Across	Along
% Changing	100%	100%
Mean Changing Value (Neurons)	1.52	-1.64

Table 6 shows interesting results. The PSE value referred to the higher-level layer is close to 1. A similar result has been found in both Green and Longo & Haggard Paper as regards the palm of the hand. In fact, from Green data PSE equal to 0.932 was obtained whereas a PSE equal to 0.967 was reported on Longo paper. This suggests that the neuronal network could reproduce the very modest orientation-dependent tactile illusion over the palm.

As regards the two-point discrimination threshold we can say it corresponded to 1.7 cm along the transversal direction whereas it was equal to 1.8 cm on the longitudinal direction.

Feed-forward Synapses

The following cases report model outcomes due to perturbing feed-forward synapses parameters.

Case 8: Decreasing Feed-forward synapses' longitudinal dimension.

As I have written in Chapter 2, in order to provide both rescaling and tactile illusion, I implemented feed-forward synapses with an oval shape. In particular, the long axis runs across the cortical area (transversal direction) whether the short one runs along the cortical area.

In Case 8 I investigated model behaviour when the short axis of the synapses from Area1 to Area2 is reduced, without changing any other parameter.

That is:

$\sigma_y^{\mathrm{W}} = 0.85\, neurons \rightarrow 0.70\, neurons$

$\sigma_x^{\mathrm{W}} = 1.70\, neurons$

$$\frac{\sigma_x^W}{\sigma_y^W} = 2 \rightarrow 2.43$$

The pattern of feed-forward synapses resulting from this modification is reported in Figure 13: the oval shape is enhanced due to a further decrease of longitudinal axis with respect to the transversal axis.

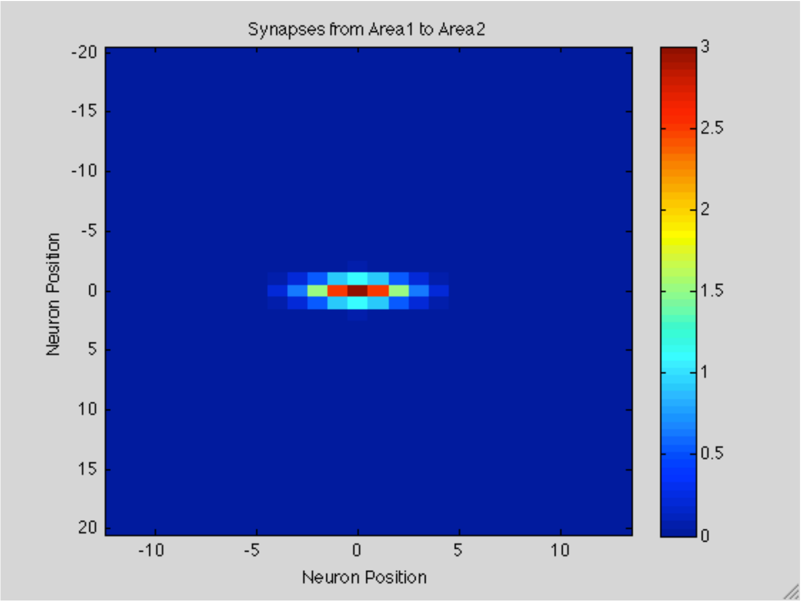


Figure 13. Pattern of feed-forward synapses. The oval shape is enhanced due to a further decrease of longitudinal axis with respect to the transversal axis.

With this pattern of feed-forward synapses, no activation in the higher-level area is elicited by an external input applied to the network.

That is, a longitudinal axis lower or equal to 0.70 neurons could not provide bubbles of activation within Area2.

Case 9: Increasing Feed-forward synapses' longitudinal dimension.

In this case, the short axis has been increased in order to obtain feed-forward synapses with a circular shape. In other words, the short axis was equal to the long one.

Hence:

$$\sigma_y^{\mathrm{W}} = 0.85\, neurons \rightarrow 1.70\, neurons$$

$$\sigma_x^{\mathrm{W}} = 1.70\, neurons$$

$$\frac{\sigma_x^{\mathrm{W}}}{\sigma_y^{\mathrm{W}}} = 2 \rightarrow 1$$

The feed-forward synapses intensity has not been perturbed.

The pattern of the modified feed-forward synapses is shown in Figure 14.

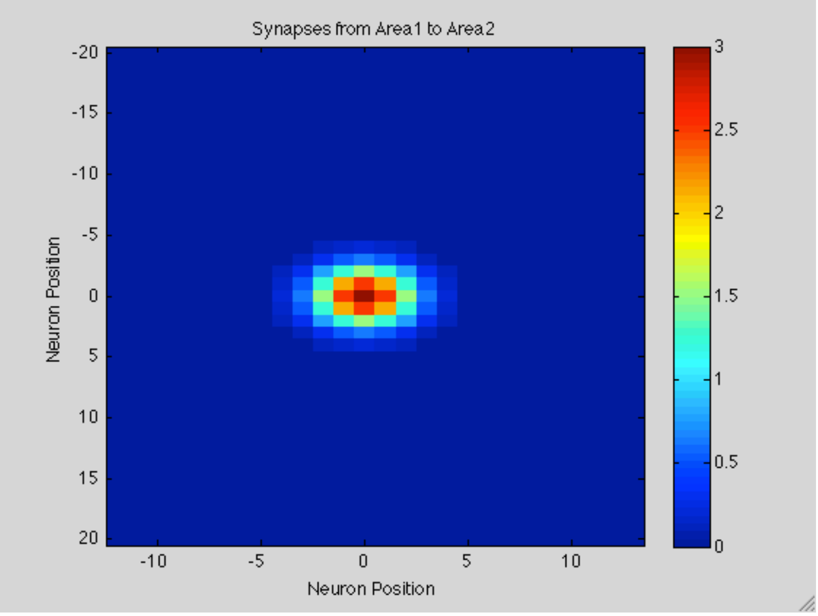


Figure 14. Feed-forward synapses have circular shape.

I think this case of study is very interesting because we can observe the output predicted by the model when the all units, composing the neuronal network, communicate each other via circular synapses. That is, both lateral and feed-forward synapses have a circular shape. In particular:

Table 7

$\mathrm{PSE}_{\mathrm{Area1}}$	$\mathrm{PSE}_{\mathrm{Area2}}$	Rescaling Effect Magnitude	Orientation-Dependent Tactile Illusion Magnitude
0.787	0.815	0.028	0.185

Data showed in Table 6 are reported again in Figure 12.

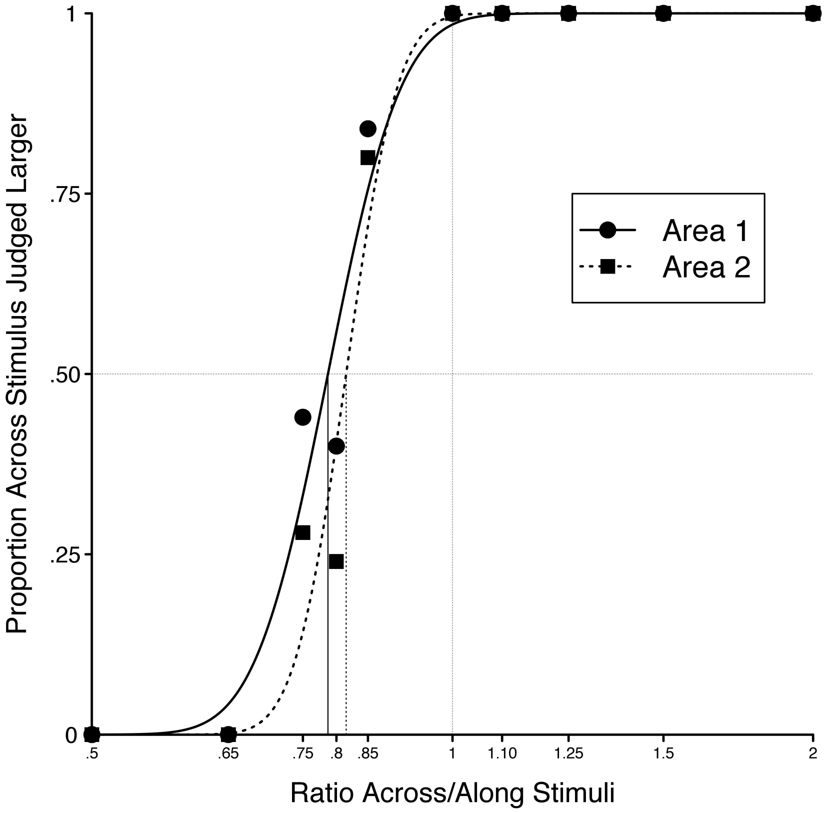


Figure 15. Model outcomes provided by circular feed-forward synapses.

Note that, PSE_{Area2} in Table 6 is lower than PSE_{Area2} obtained with basal parameter values. In fact, as the synapses enlarged their size, the number of neurons sitting between the two balls of activation did not increase along longitudinal direction, preserving the same value provided within the first layer. So, balls of activation preserved their longitudinal size from Area1 to Area2. Conversely, across the cortical area, neurons encoding the perceived distance in Area 2 were fewer than those within Area1. In other words, balls of activation in Area2 increased in their transversal size, as a consequence, distance between them became smaller.

On the overall, balls of activation within the second layer were bigger than those provided by the model using parameter settings listed in Chapter 2.

	Across	Along
% Changing	100%	70%
Mean Changing Value (Neurons)	1.13	1

Case 10: Decreasing Feed-forward synapses' transversal dimension.

Here, I have analysed model behaviour when decreasing the standard deviation of the feed-forward synapses in the across direction. This means reducing the oval shape of these synapses (indeed, in basal conditions the standard deviation of the synapses in the across direction is larger than in the along direction).

In other words, the intent was to set σ_x^{W} at the same value of σ_y^{W}. Anyway, these settings provided very tiny feed-forward synapses, which means no balls of activation within the second layer.

So, σ_x^{W} was set at the value 1.20 neurons because it is the smallest value that provide pattern of activation in the higher-level layer.

Hence:

$$\sigma_y^{\mathrm{W}} = 0.85\, neurons$$

$$\sigma_x^{\mathrm{W}} = 1.70\, neurons \rightarrow 1.20\, neurons$$

$$\frac{\sigma_x^{\mathrm{W}}}{\sigma_y^{\mathrm{W}}} = 2 \rightarrow 1.41$$

By observing Figure 16 we can note that only the four neighbourhood neurons right next to the considered one, received a noticeable excitation. The excitation effect was clearly reduced.

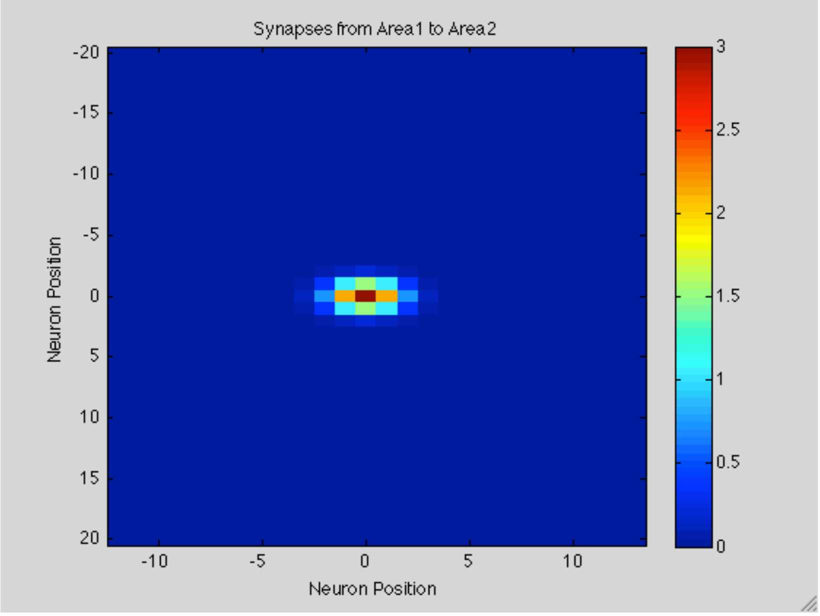


Figure 16. By decreasing the transversal axis of the synapses the excitation effect is clearly reduced. In particular, only the four neighbourhood neurons right next to the considered one, received a noticeable excitation.

With synapses from Area1 to Area2 shaped in this way, outputs provided by the model referred to Area2 were small balls of activation. This means, perceived distance became larger when shifting from the first layer to the second one.

	Across	Along
% Changing	100%	100%
Mean Changing Value (Neurons)	-2.10	-3.95

Differences in term of perceived distance are reported both in Table 7 and Figure 17 too.

Table 5

PSE$_{Area1}$	PSE$_{Area2}$	Rescaling Effect Magnitude	Orientation-Dependent Tactile Illusion Magnitude
0.778	0.785	0.007	0.215

By having a look at the table it easy to say this case provided similar results to the previous one. In fact, decreasing σ_x^W involved a great decrement of the balls' sizes.

As in the case before, PSE_{Area2} was lower than that one obtained with basal parameter values (see Chapter 3).

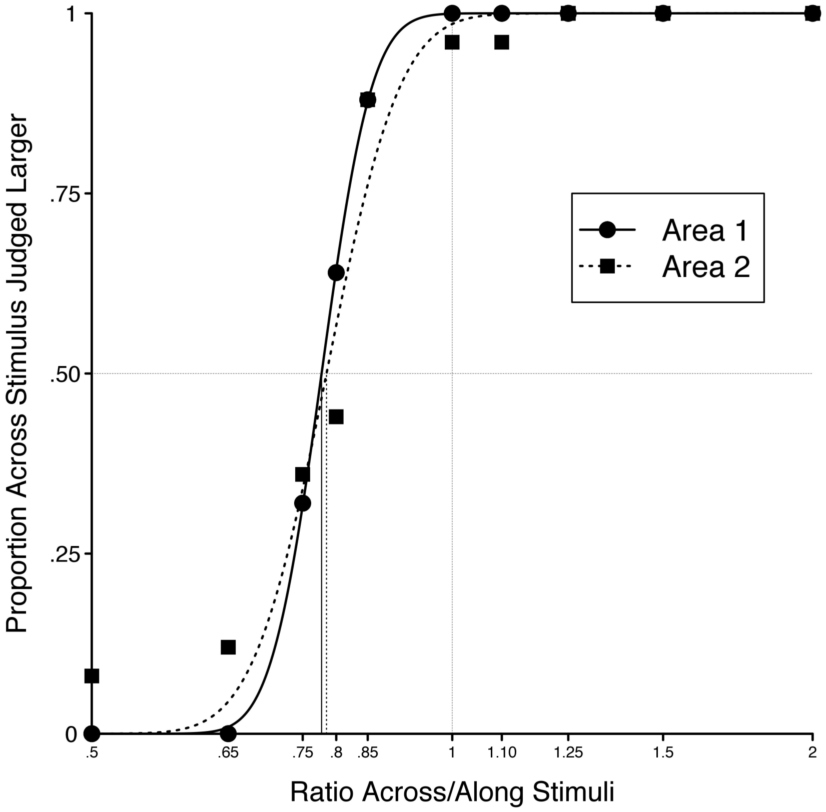


Figure 17. The neuronal network did not provide a high rescaling magnitude. Moreover PSE_{Area2} present a value, which is similar to that one found by Longo & Haggard as regards the dorsum of the hand.

The main difference between the present and the previous case stands on the comparison between PSEs of the first layer and the second one. PSEs have similar values. So, even if the along MCV is almost two times the across one, there is not a noticeable rescaling effect. Moreover, PSE_{Area2} is close to $PSE_{L\&H}$ (0.729) as regards the dorsum of the hand.

A two-point discrimination threshold equal to 1 was detected over the transversal orientation whereas it was equal to 1.4 cm on the opposite direction.

Case 11: Increasing Feed-forward synapses' transversal dimension.

In the following I will report final results due to synapses with a longer transversal axis.

So, across cortical areas, excitatory effect is greater.

Here the settings:

$$\sigma_y^{\mathrm{W}} = 0.85\, neurons$$

$$\sigma_x^{\mathrm{W}} = 1.70\, neurons \rightarrow 2.70\, neurons$$

$$\frac{\sigma_x^{\mathrm{W}}}{\sigma_y^{\mathrm{W}}} = 2 \rightarrow 2.35$$

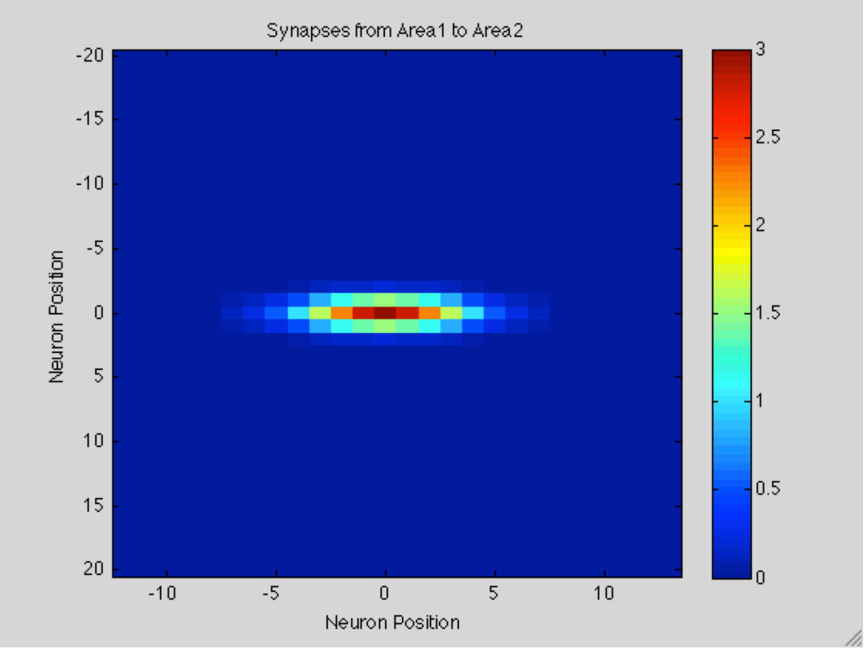


Figure 18. The anisotropy in feed-forward synapses shape is increased as the transversal axis became larger.

It is expected that, by incrementing the transversal dimension of the feed-forward synapses, perceived distance in the transversal

orientation gets smaller from Area1 to Area2, due to an increment of the transversal size of the balls of activation.
Data below support this expectation.

	Across	**Along**
% Changing	100%	100%
Mean Changing Value (Neurons)	1.2	-2.01

PSEs values as well as Rescaling Magnitude Effect are very similar to those reported in Case 7. In this case too, the model could simulate results observed over the palm (that is a very small orientation effect).

Table 6

PSE$_{Area1}$	**PSE$_{Area2}$**	**Rescaling Effect Magnitude**	**Orientation-Dependent Tactile Illusion Magnitude**
0.787	0.930	0.142	0.07

Note that (see Figure 16), the increment of σ_x^W produces a shift of the curve more on the right side of the chart providing a higher PSE$_{Area2}$.

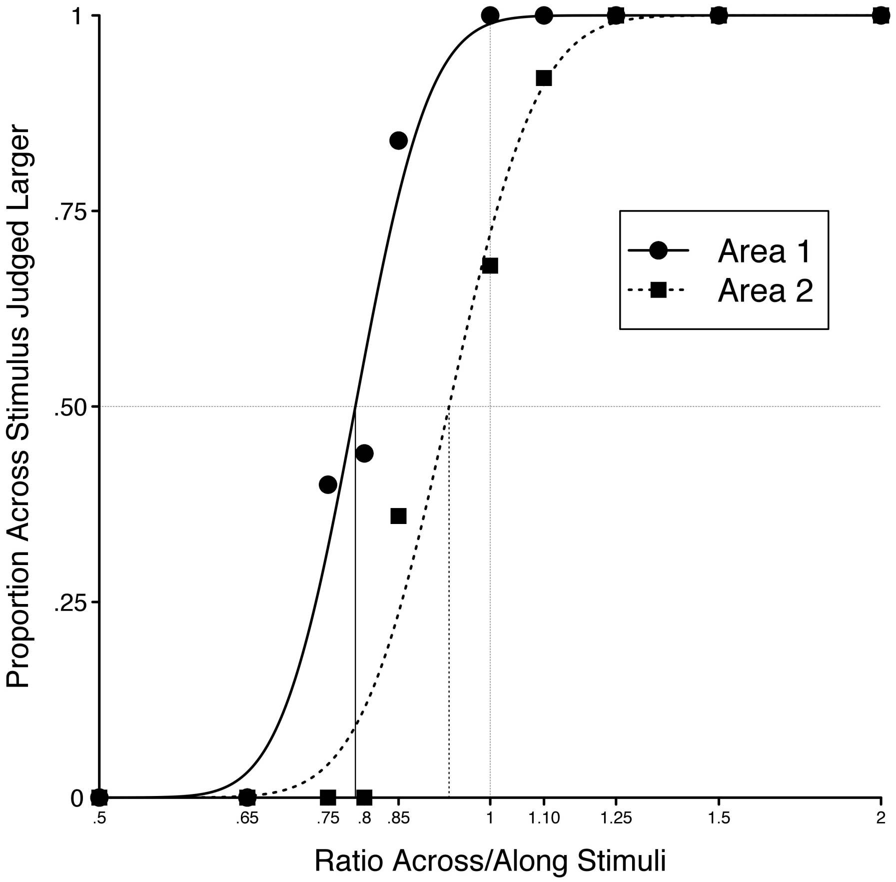


Figure 19. Proportion across stimulus judged larger than longitudinal one by considering any simulated area. Note that PSE$_{\text{Area2}}$ is very similar to that one found by Green and Longo as regards the palm.

Obviously, σ_x^{W} set in this way provided, at short distances (applied distances lower than 2 cm), a better discrimination along the hand rather than across the hand. This effect was not observed for distances greater than 2 cm. That is, 2PDT was equal to 2 cm across the hand and 1.5 cm along the hand.

Case 12: Decreasing Feed-forward synapses' dimensions.

In this case I have perturbed both σ_y^{W} and σ_x^{W} in order to asses if little changing of their values could play an important role in the neuronal network.

In particular:

$\sigma_y^{\mathrm{W}} = 0.85\, neurons \rightarrow 0.75\, neurons$

$\sigma_x^{\mathrm{W}} = 1.70\, neurons \rightarrow 1.60\, neurons$

$\frac{\sigma_x^{\mathrm{W}}}{\sigma_y^{\mathrm{W}}} = 2 \rightarrow 2.13$

Clearly, the shape of the synapses did not differ so much from the condition of basal parameter values.

It is expected that by decreasing σ_y^{W} as well as σ_x^{W}, balls of activation within Area2 get shrink at both orientations. So, the hypothesis I have made is that both the across MCV and the across %C could be a *bit lower* with respect to the basal condition. Same considerations have been made for the longitudinal orientation. Hence, cumulative Gaussian functions could present less bias, that is, $\mathrm{PSE}_{\mathrm{Area2}}$ should be smaller.

Now, if we look at the table below and at the picture, we can note that previous considerations are verified.

Table 7

$\mathrm{PSE}_{\mathrm{Area1}}$	$\mathrm{PSE}_{\mathrm{Area2}}$	**Rescaling Effect Magnitude**	**Orientation-Dependent Tactile Illusion Magnitude**
0.757	0.799	0.042	0.201

$\mathrm{PSE}_{\mathrm{Area2}}$ is close to 0.80 which is smaller than 0.851 (this is the $\mathrm{PSE}_{\mathrm{Area2}}$ value reported in Chapter 3). In fact, an increment of $\frac{\sigma_x^{\mathrm{W}}}{\sigma_y^{\mathrm{W}}}$ value, suggested each ball of activation gets larger more on the transversal size than on the longitudinal one.

As a consequence, there was more orientation-dependant tactile illusion by using these settings.

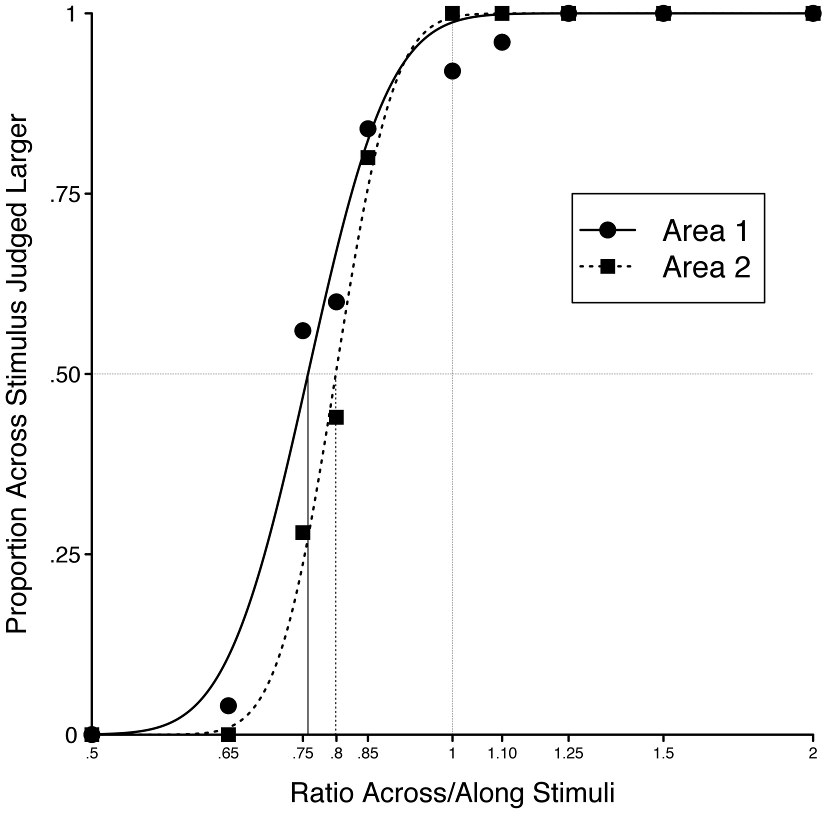


Figure 20. Final results obtained by the model.

Anyway, the model did not provide the expected results in term of %C. In fact, by decreasing the standard deviations of a factor equal to 0.10, the across %C gets the maximum value.

	Across	**Along**
% Changing	100%	100%
Mean Changing Value (Neurons)	-1.76	-2.54

Case 13: Increasing Feed-forward synapses' dimensions.

What happens if σ_y^{W} and σ_x^{W} increase of a factor equal to 0.10?

$\sigma_y^{\mathrm{W}} = 0.85\, neurons \rightarrow 0.95\, neurons$

$\sigma_x^{\mathrm{W}} = 1.70\, neurons \rightarrow 1.80\, neurons$

$$\frac{\sigma_x^{\mathrm{W}}}{\sigma_y^{\mathrm{W}}} = 2 \rightarrow 1.89$$

As expected, the across %C values become smaller as well as the along MCV.

Anyway, $\mathrm{PSE}_{\mathrm{Area2}}$ remains substantially unaltered.

Table 8

$\mathrm{PSE}_{\mathrm{Area1}}$	$\mathrm{PSE}_{\mathrm{Area2}}$	**Rescaling Effect Magnitude**	**Orientation-Dependent Tactile Illusion Magnitude**
0.793	0.860	0.067	0.140

The only advantage reflects the across %C which is very small.

	Across	**Along**
% Changing	10%	100%
Mean Changing Value (Neurons)	-1	-1.55

Clearly this case represents the opposite version of the previous one. So, as the $\frac{\sigma_x^{\mathrm{W}}}{\sigma_y^{\mathrm{W}}}$ ratio became lower, each ball of activation presented a greater increment of their longitudinal size rather than the transversal one. In fact, $\mathrm{PSE}_{\mathrm{Area2}}$ is slightly higher than that one found in Chapter 3. Obviously the difference is not so high because the ratio was only a bit higher.

Moreover, there is not difference between the transversal and the longitudinal two-point discrimination threshold (in both cases it results equal to 1.5 cm)

Finally, I reported cumulative Gaussian function in Figure 21.

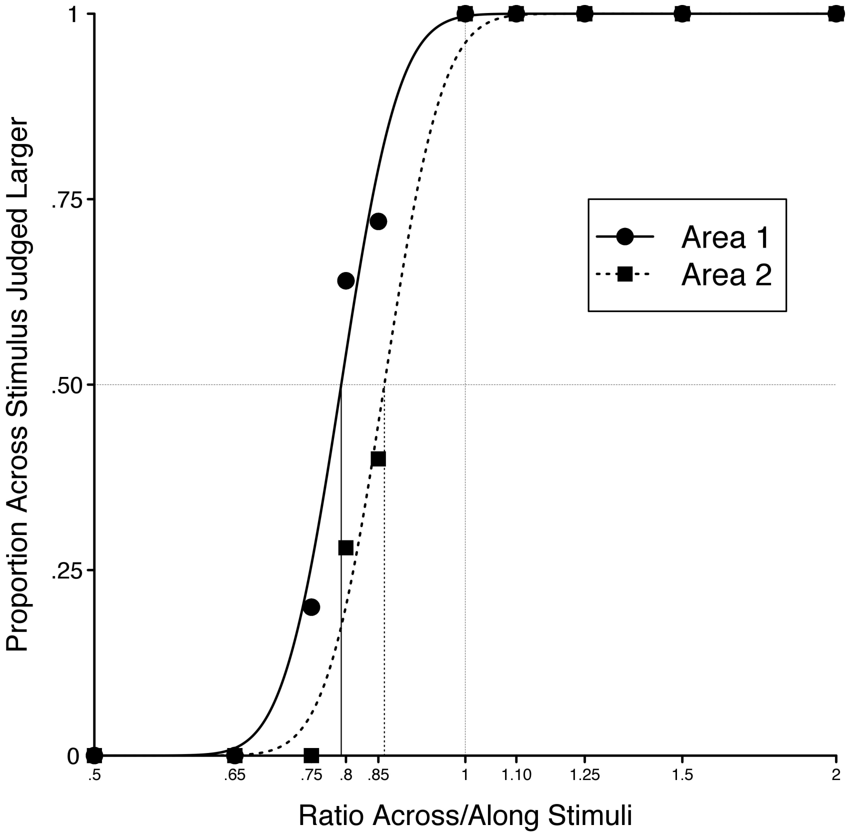


Figure 21. The settings provided results, which were similar to those found thanks to the basal parameter value.

Case 14: Increasing the Gaussian function's intensity.

I investigated model behaviour by increasing the intensity of the Gaussian function. I expect results similar to those obtained in case 10 (as concern %C), but maintaining two different 2PDT..

In fact, σ_y^{W} and σ_y^{W} having the basal values, should guarantee a good discrimination between the transversal and longitudinal threshold. Intensity of feed-forward synapses was increased by 1.

$$W_0^{f \to s} = 3 \to 4$$

Unfortunately, changing $W_0^{f \to s}$ do not provide interesting results. In fact, across %C values is equal to the 32% (which is similar to that value reported in Chapter 3). Moreover, this setting tends to preserve the same perceived distance value in both Area1 and Area2 when

stimuli running along the hand were simulated. That is, along MCV is a bit more than 1 neuron and %C is not equal to the 100%.
Hence:

	Across	**Along**
% Changing	32%	97%
Mean Changing Value (Neurons)	1	-1.12

Moreover, the lower applied distance that can be discriminated is the same at both orientations and it corresponds to 1.5 cm.
Results about rescaling and PSEs are reported below.

Table 9

$\mathbf{PSE_{Area1}}$	$\mathbf{PSE_{Area2}}$	**Rescaling Effect Magnitude**	**Orientation-Dependent Tactile Illusion Magnitude**
0.773	0.815	0.042	0.185

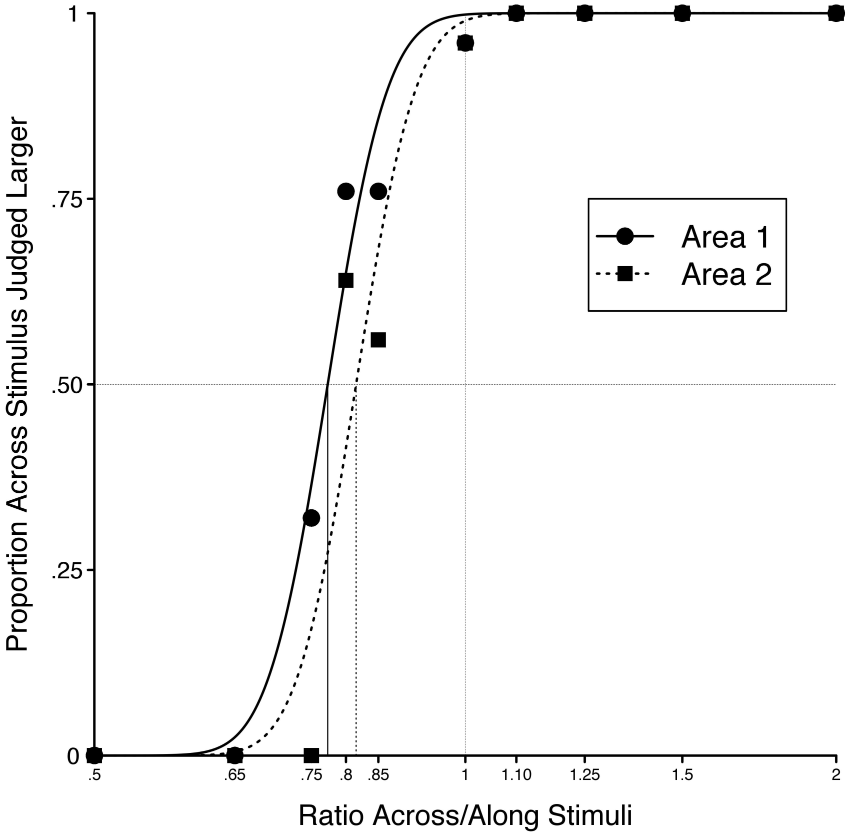


Figure 22. The settings provided results, which were similar to those found thanks to the basal parameter value.

Case 15: Decreasing the Gaussian function's intensity.

Here, I decreased the intensity by a factor equal to 1.
That is:

$$W_0^{f\to s} = 3 \to 2$$

What is important is that no patterns of activation were found within Area2.
Obviously, I did not try to assign to $W_0^{f\to s}$ values inside the range 2÷3. In fact, an intensity value lower than 3 but sufficient to generate activation in the higher-level layer, cannot provide interesting results in term of rescaling.

Activation Threshold

Another parameter that plays a key role in the neuronal network is the activation threshold. In fact, the output of the network depends on that value.
Neurons activated over the threshold are considered as maximally activated and so they compose the bubbles of activation in each Area. So, the higher is the threshold, the fewer neurons represent the bubbles. As a consequence, distance between them becomes higher. Conversely, by decreasing the value of this parameter, neurons encoding for the perceived distance become fewer as more neurons may present activation value higher than the threshold.
So, I analyse if changing of the activation threshold might change the behaviour of the neuronal network.
That is, I investigated model behaviour by setting different values of this parameter, in particular by decreasing this parameter.
The following four cases report model outcomes by setting the activation threshold at value 0.7, 0.5, 0.3, 0.1.

Case 16: Threshold of Activation is equal to 0.7.

By decreasing the threshold of activation of a factor equal to

0.2, the cumulative Gaussian function representing final results provided by the neuronal network, are reported below.
Note that PSE_{Area1} as well as PSE_{Area2} are close to those obtained by setting the threshold at 0.9.

Table 10

PSE_{Area1}	PSE_{Area2}	Rescaling Effect Magnitude	Orientation-Dependent Tactile Illusion Magnitude
0.767	0.846	0.079	0.154

The results listed in the table above demonstrate there is not a noticeable difference in term of PSEs (with respect to activation threshold at 0.9).

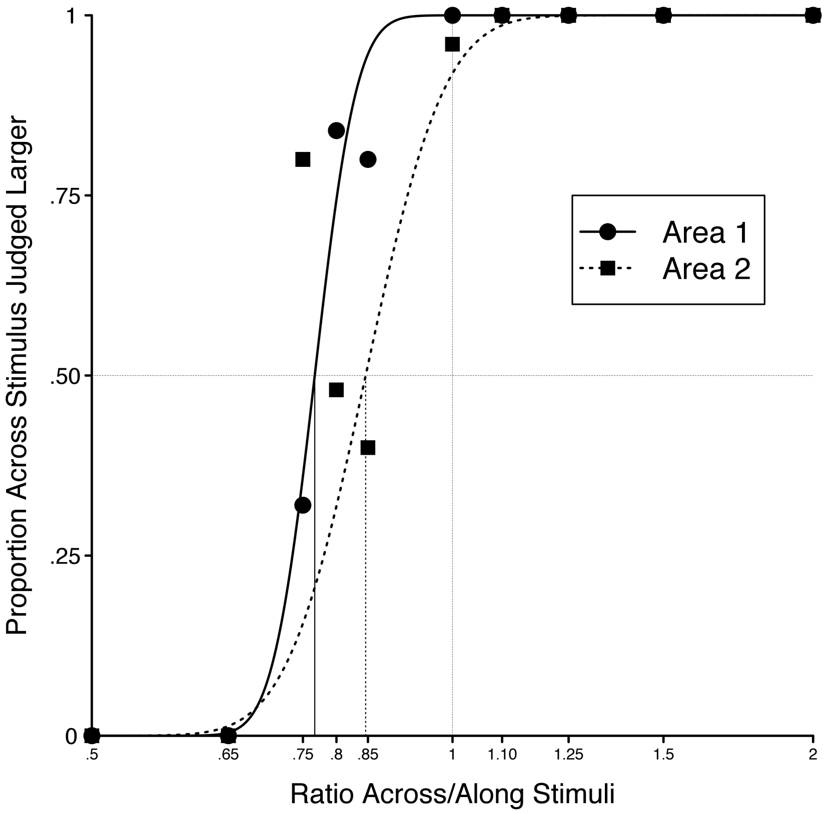


Figure 23. There is not a noticeable discrepancy between PSEs and those ones reported in the previous chapter.

Anyway, neurons with an activation value greater than the 70% of the maximal activation were considered as maximally activated. As a consequence, this setting reduces the number of neurons sitting between the bubbles of activation. Clearly the consideration was satisfied along the hand as well as across the hand. It means that the across MCV and the along one could decrease.

	Across	**Along**
% Changing	3%	100%
Mean Changing Value (Neurons)	1	1.73

The along MCV decreased about 1 neurons (it was 2.57 neurons by considering an activation threshold equal to 0.9). Obviously, the across MCV could not become lower than 1 neurons. Anyway, we can note %C is very low demonstrating there are only few trials that did not preserve the perceived distance from Area1 to Area2.

However the main important noticeable effect provided by decreasing the threshold is due to the two-point discrimination.

In fact, focusing on short distances, bubbles of activation were sitting close to each other So, it may happens that, by decreasing the threshold, all neurons present a value of activation higher than the threshold. As a consequence it is not possible to discriminate the two external stimuli.

In this case of study the two-point discrimination threshold is equal to 1.3 cm in both the investigated orientation. So, there is not a discrimination between the along and across orientation.

Case 17: Threshold of Activation is equal to 0.5.

Decreasing to 0.5 the value of the threshold, the effects explained in the previous paragraph could be emphasised. In order to confirm this consideration I have reported below %C and MCV.

	Across	**Along**
% Changing	3%	100%

Mean Changing Value (Neurons)	1	1.42

For the across orientation, the same results as case before are obtained. As to the longitudinal direction, the MCV is further decreased. *This means, within Area2 bubbles increased their longitudinal size preserving the transversal one.*

In fact, since along MCV decreases, there was less difference in term of perceived distance between Area1 and Area2 at this specific orientation.

Focusing on the longitudinal direction, perceived distance within Area2 became lower than that one provided with an activation threshold equal to 0.9. As a consequence, a lower PSE_{Area2} should be expected.

Table 13 shows the obtained results.

Table 11

PSE_{Area1}	PSE_{Area2}	Rescaling Effect Magnitude	Orientation-Dependent Tactile Illusion Magnitude
0.763	0.824	0.060	0.176

Note that Rescaling Effect Magnitude is lower than that one in the case before, whereas the Orientation-Dependent Tactile Illusion is greater.

Moreover, PSE referred to Area2 is slightly decreased (from 0.846 to 0.824) whereas there is not a noticeable difference as regard PSE of Area1.

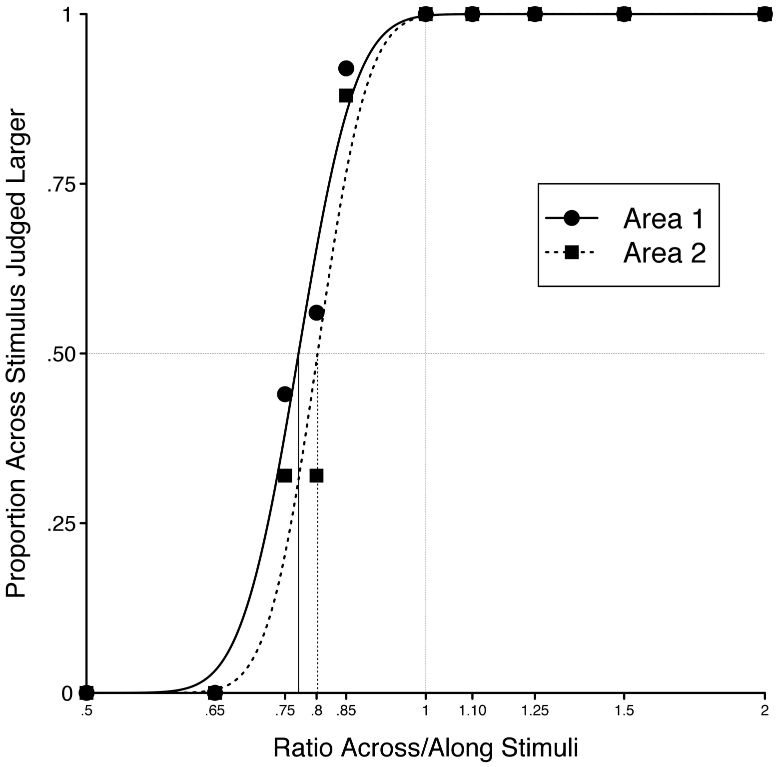


Figure 24. Area2 cumulative Gaussian function presents more bias than the correspondent in Figure 1. In fact, PSE$_{\text{Area2}}$ was lower.

Moreover not noticeable differences were observed as regards the two-point discrimination threshold. It corresponded to 1.3 cm across the hand whereas it was 1.4 cm along the hand.

Case 18: Threshold of Activation is equal to 0.3.

Previous cases suggest an interesting observation: the lower is the threshold the lower is the PSE$_{\text{Area2}}$. This effect was due to the shape of the bubbles of activation. They have an oval shape with the long axis running across the cortical area. Anyway, by focusing on the edges of the bubbles, there is a better contrast over the “vertical” edges rather than over the “horizontal” ones. Clearly, vertical edges defined the transversal size whereas the horizontal edges defined the longitudinal size. Focusing on the vertical direction, there is not as good contrast as along the horizontal orientation. This means neurons sitting right next to those composing the border of a bubble (horizontal edged), have an activation value closer to the basal activation threshold. Take a look at the figure below for a better understanding.

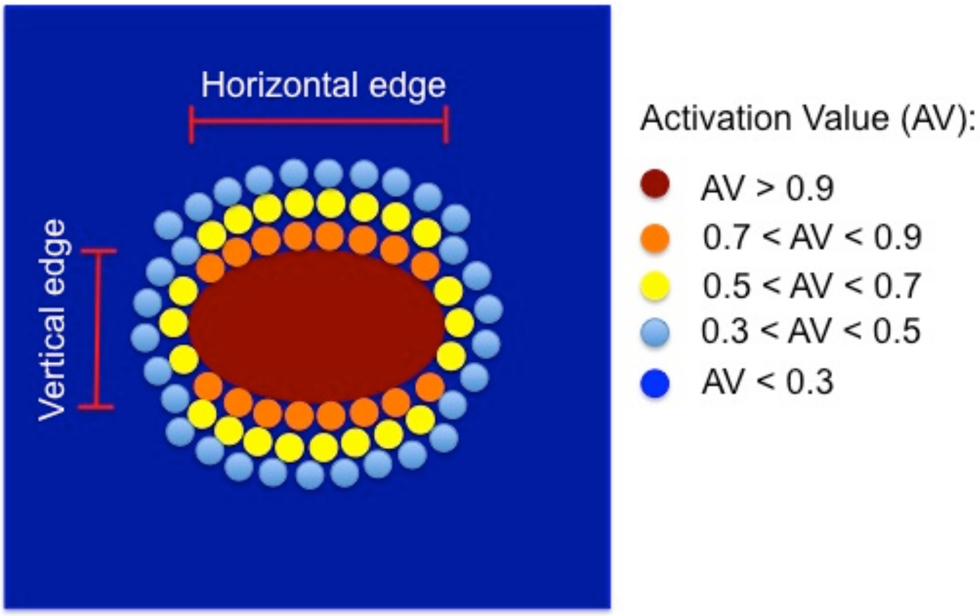


Figure 24. Representation of a bubble of activation. Vertical edges are less blurred than the horizontal ones.

Figure 24 is clearly a simplification of the real case but it is helpful in order to understand that vertical edges are less blurred than the horizontal ones.

Finally, outputs from the neuronal network are reported below.

Table 12

PSE$_{Area1}$	PSE$_{Area2}$	Rescaling Effect Magnitude	Orientation-Dependent Tactile Illusion Magnitude
0.771	0.802	0.031	0.198

Note that PSE$_{Area2}$ is lower than that one computed in the case before. As rescaling effect decreased from case to case cumulative Gaussian function tent to be closer to each other. Figure 25 clearly demonstrated the effect.

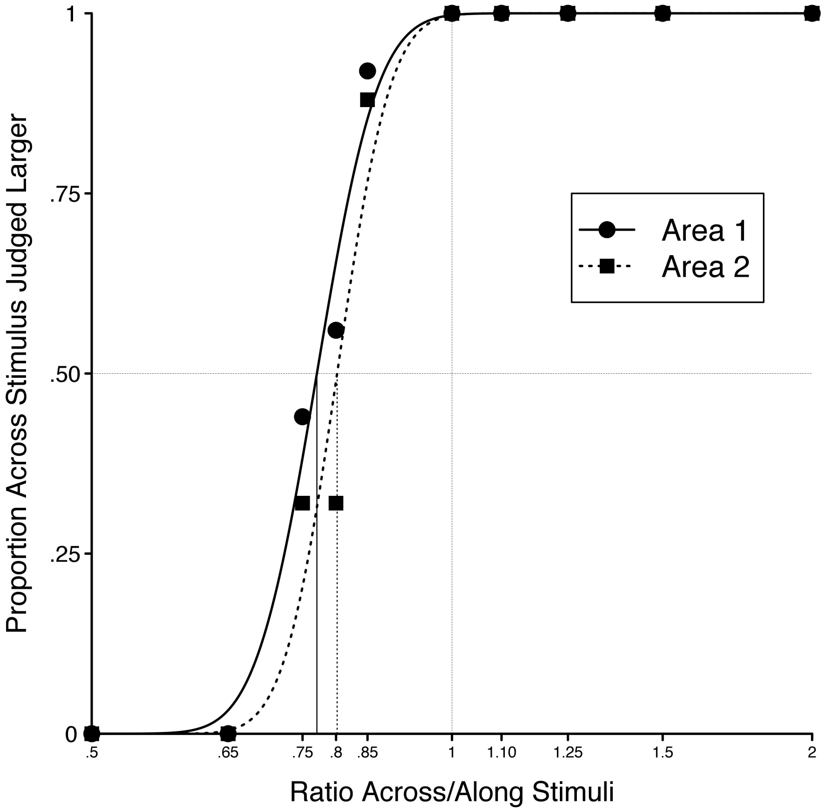


Figure 25 . Due to less rescaling, cumulative Gaussian functions tent to be closer to each other.

By considering an activation threshold equal to 0.3 there are not noticeable differences, in term of perceived distance, between Area1 and Area2 in both the investigated orientation.

In fact:

	Across	**Along**
% Changing	2%	71%
Mean Changing Value (Neurons)	1	1

Note that along MCV has the same value of across MCV. Anyway, %C is much greater in the along direction than across direction. Moreover %C is not equal to the 100%.

Finally, two-point discrimination thresholds equal to the previous case were detected.

Case 19: Threshold of Activation is equal to 0.1.

By setting the threshold of activation at 0.1 an interesting effect was observed. In fact, comparing the case with the previous ones, we can note transversal perceived distance was not preserved from Area1 to Area2. This means, bubbles of activation did not preserve the across size. As a consequence they became larger along that orientation. Same considerations where satisfied over the along direction.

Hence:

	Across	Along
% Changing	100%	92%
Mean Changing Value (Neurons)	1.35	1

Note along %C as well as along MCV did not differ compared with the previous case. Obviously we could not say the same as regards the opposite direction. In this way, the rescaling assumption was not satisfied.

So, it easy to understand that the transversal perceived distance decreased from Area1 to Area2. Hence, PSE_{Area2} became higher than what was reported in the previous paragraphs.

Table 13

PSE_{Area1}	PSE_{Area2}	Rescaling Effect Magnitude	Orientation-Dependent Tactile Illusion Magnitude
0.756	0.849	0.093	0.151

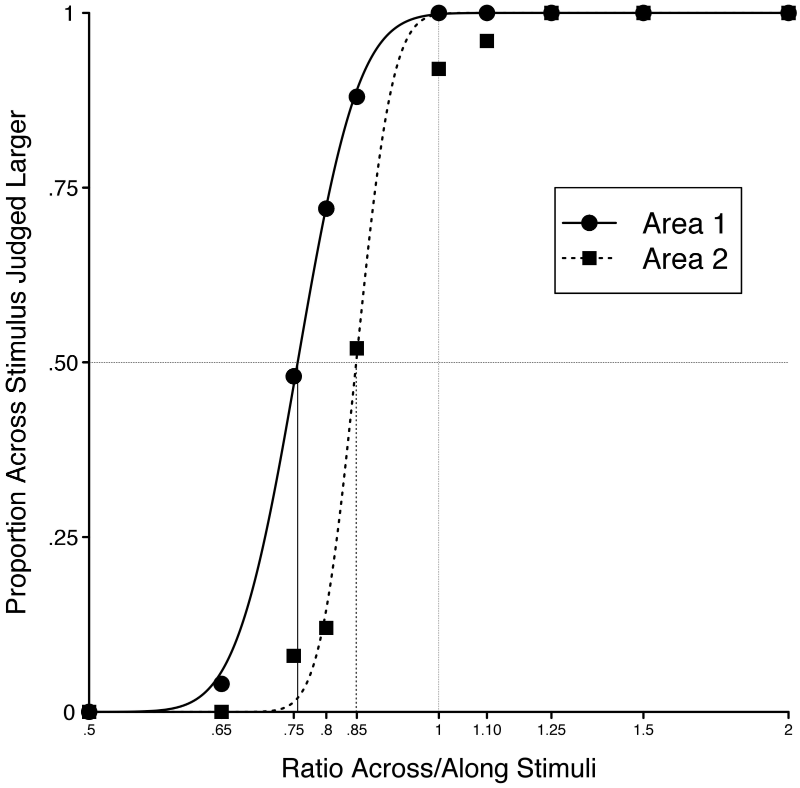


Figure 26. Model outcomes by considering an activation threshold equal to 0.9.

In addition, thanks to this setting, two-point discrimination thresholds increased. Across the hand two external stimuli could be discriminated if they were spaced 1.4 cm each other whereas along the hand a distance equal to 1.5 cm was necessary in order to provide the same effect.

Receptive Fields' shape

Case 20: Increasing the long axis of the RFs.

In this case I investigated the neuronal network behaviour by changing the shape of the RFs. In particular amount of anisotropy was increased. This means that the ratio between the long axis and the short one became higher.

Hence:

$$\sigma_y^{\Phi} = 0.30\ cm \to 0.45\ cm$$

$$\sigma_x^{\Phi} = 0.15\ cm$$

$$\frac{\sigma_y^{\Phi}}{\sigma_x^{\Phi}} = 2 \to 3$$

The figure below represents a RF of a generic neuron within the first layer.

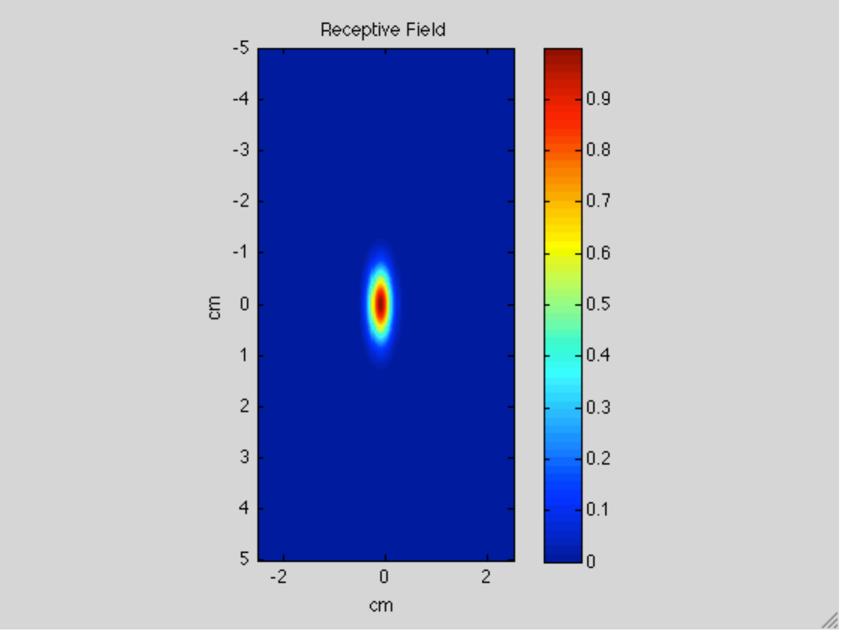


Figure 27. RF of a generic neuron within the first layer. By increasing the long axis, anisotropy effects are greater.

The setting provided results reported in the table below:

Table 14

PSE_{Area1}	PSE_{Area2}	Rescaling Effect Magnitude	Orientation-Dependent Tactile Illusion Magnitude
0.670	0.793	0.123	0.206

As we can note PSE within Area1 strongly differ from that one in Area2. The model provided rescaling with the intent to obtained perceived distances within Area2, which could be more similar to the physical distances.

The figure below gives us an illustration of the final results.

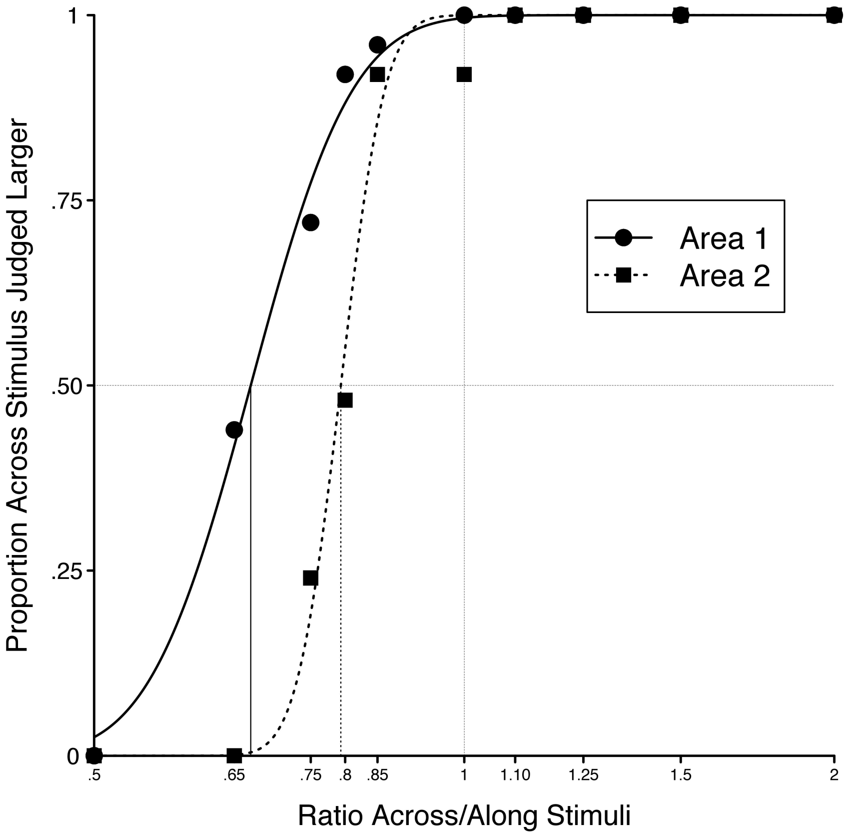


Figure 28. **The model rescales perceived distance within Area1. The final result is an increment of the PSE from Area1 to Area2.**

As RFs have been increased in their longitudinal size, the finals results are not unexpected. In fact, the settings provided an increment of the longitudinal size of the bubble of activation without noticeable changing in term of the opposite direction. As a consequence, PSE_{Area2} obtained with these parameters is smaller than those obtained with basal parameter values..

This case provides a better approximation of what Longo found by investigated the dorsum of the hand (PSE=0.729).

Moreover, rescaling is due to an enhancement of the discrimination only along the longitudinal direction, which presents the worse sensory acuity.

	Across	Along
% Changing	2%	100%
Mean Changing Value (Neurons)	-1	-2.56

This strong anisotropy in RFs shape provided better discrimination across the hand rather than along the hand. In fact, the 2PDT was equal to 1.3 cm across the hand and 2 cm along the hand.

These effects could clearly be increased if σ_y^Φ becomes even higher. That is:

$$\sigma_y^\Phi = 0.30\ cm \rightarrow 0.6\ cm$$

$$\sigma_x^\Phi = 0.15\ cm$$

$$\frac{\sigma_y^\Phi}{\sigma_x^\Phi} = 2 \rightarrow 4$$

These settings provided final results showed in the table as well the figure below.

Table 15

PSE_{Area1}	PSE_{Area2}	Rescaling Effect Magnitude	Orientation-Dependent Tactile Illusion Magnitude
0.628	0.746	0.118	0.252

The results are very interesting as PSE value within Area2 is very close to 0.729, which is what found by Longo & Haggard as regards the dorsum of the hand.

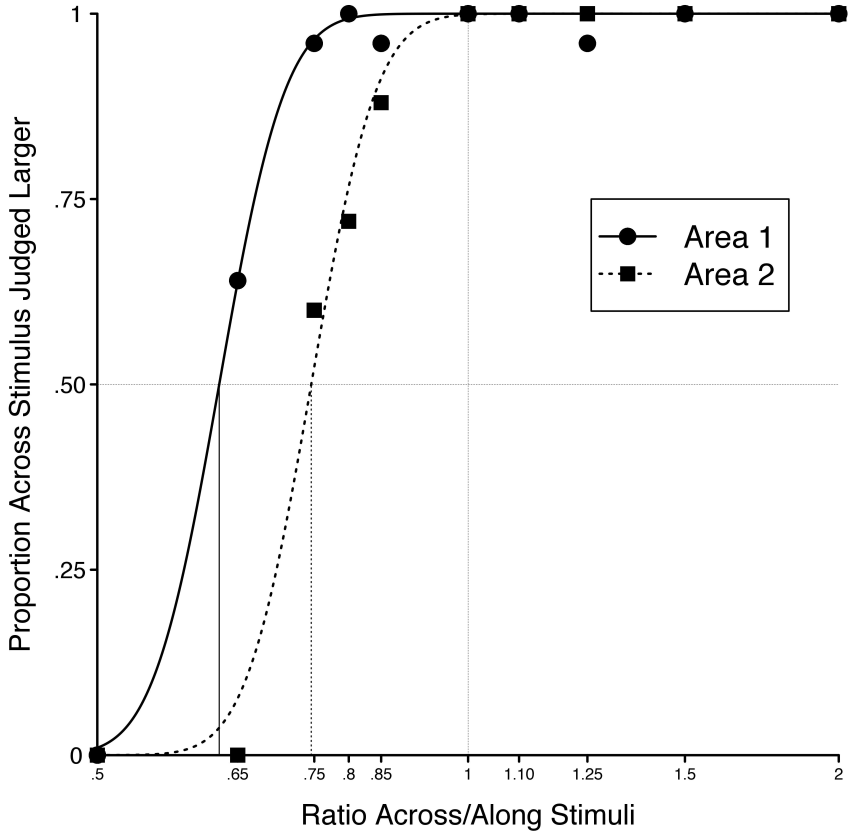


Figure 6. There are not noticeable differences between PSE_{Area2} and $PSE_{L\&H}$.

As in the previous case, rescaling is due to an enhancement of the discrimination only along the longitudinal direction, which presents the worse sensory acuity.

	Across	**Along**
% Changing	9%	100%
Mean Changing Value (Neurons)	-1	-3.05

This strong anisotropy in RFs shape provided better discrimination across the hand rather than along the hand. In fact, the 2PDT was equal to 1.4 cm across the hand and 2.6 cm along the hand.

Considerations

Previous cases demonstrate that the neuronal network behaviour strongly depends on the parameters referred to the feed-forward synapses. In particular, σ_y^W and σ_x^W, which were responsible of the oval-shape of the synapses, played an important rule. In fact, decreasing transversal dimension produce the effect of diminishing rescaling effect (that is the two sigmoidal curve in Area 1 and Area 2 tend to become closer). This modification, indeed, acts in the direction of reducing the anisotropy of feed-forward synapses shape. This provided PSE values within Area2 much more similar to the value found by Longo as regards the dorsum of the hand.

Conversely, increasing transversal dimension produce the effect of augmenting rescaling effect (that is the two sigmoidal curve in Area 1 and Area 2 tend to become farther apart). This change, indeed, act in the direction of incrementing the anisotropy of the shape of feed-forward synapses. As a consequence, PSE values within Area2 was much more similar to that value found by Longo and Green as regards the palm.

Similar results were obtained by changing the shape of the lateral synapses within Area2. In fact, by decreasing the standard deviation of the inhibitory Gaussian function bubbles of activation became bigger. This produced the effect of augmenting rescaling effect. The change, indeed, act in the direction of reducing transversal perceived distance more than the longitudinal one (as bubbles of activation become larger in the transversal direction than in the longitudinal direction). So, PSE value within Area2 was very close to 1 as found by Longo and Green as regards the palm. Conversely, increasing the lateral inhibition produces the effect of diminishing rescaling effect (that is the two sigmoidal curve in Area 1 and Area 2 tend to become closer). As a consequence PSE value within Area2 was much more similar to that value found by Longo as regards the dorsum of the hand.

Conclusion

Perception of tactile distance on a single skin surface changes with stimulus orientation: that is, the physical distance between two tactile punctual stimuli is judged larger across a skin surface rather than along the skin surface itself. The illusion is due to differences in receptor density, differences in dimension and shape of receptive fields and cortical magnification effects.

The investigation of this illusion on different body regions (Green, Percpept Pshycophys 31, 315-323, 1982; Longo & Haggard, J.Exp.Psychol. Hum Percept Perform 37: 720-726, 2011) provided a mean PSE value (ratio for which the two investigated distances are judged equal) equal to 0.84. This means that for the along distance to be perceived equal to the across distance, it is necessary that it is about 20% greater than the across distance. This result indicates that the illusion is smaller than what expected by simply considering the difference in receptor density and anisotropy in receptor field shape and it suggests that a sort of rescaling process is performed in the cortex in order to try to maintain constant distance perception. Moreover, the greater is the applied distance, the greater is the tactile illusion.

Aim of the present work was the implementation of a neuronal network that simulates mechanisms involved in tactile perception and tactile illusion as well. In the model we hypothesized that tactile information is processed at two different levels, corresponding to two different neuronal layers. In particular, we assumed the lower-level layer (Area1) contains a distorted tactile representation created by the integrations of tactile inputs coming from the skin; the higher-level layer (Area2) acts in order to reduce distortion and to improve tactile representation of the first layer (that is operates a rescaling process). I hypothesize the higher-level layer may operate rescaling along both the investigated orientations with higher effects on the longitudinal orientation.

Each area is composed by 41x26 units and encoded for a 10 cm x 5 cm skin surface. Units communicate each other via lateral synapses that present a Mexican hat shape. Neurons in Area1 are characterized by receptive fields with an anisotropic shape, that is more elongated along the longitudinal direction. Another hypothesis I have considered is that connections between Area1 and Area2 are due to excitatory feed-forward synapses with oval shape. In particular, the long axis runs across the neuronal layer whereas the short axis runs along the layer providing the rescaling assumption cited before. As a simplification, feedback synapses were not implemented within the model. The application of two external stimuli produces two bubbles of activation within each layer. The pattern of activation (dimension of the bubbles and distance between the bubbles) within the first layer depends on the receptive field and lateral synapses, whereas in the second layer on the lateral synapses and feed-forward synapses. Moreover, due to external stimuli represent pattern of activation within the layers.

An important point concerns how to read out network output. In order to obtain network output in terms of perceived distance, we assumed that the perceived distance is codified by the number of inactivated neurons sitting between the two bubbles of activation.

I investigated behaviour of the neuronal network by setting different ratio values of applied distances (across distance/along distance). In particular I have considered two different case studies so that in the first one, the distances applied along the two orientations were smaller on the average (3 cm) than the distances applied in the second case study (average equal to 4 cm).

PSE value referred to Area1 in both cases was significantly lower than 0.84 (mean PSE by Green) and equal to 0.78 (this value was obtained by setting RF shape in agreement with the physiological literature). PSE equal to 0.78 indicates that a rescaling process of the perceived distance is necessary in order to reproduce a more physiological behaviour. Concerning Area2, the model provided a PSE value equal to 0.88 in the first case study and a PSE value equal to 0.85 in the second one demonstrating tactile illusion increases with the applied distance. These values are similar to 0.84 PSE value reported in the literature. These results suggest the model could reproduce on the average mechanisms involved in tactile perception and orientation-dependent tactile illusion.

Moreover, by changing certain parameter values, the neuronal network simulates the illusion at specific body regions. In fact, by incrementing the inhibitory standard deviation of lateral synapses within Area2, PSE_{Aresa2} becomes equal to 0.77 whereas it is equal to 0.78 by decreasing the long axis of the feed-forward synapses. These results suggest the neuronal network reproduces the orientation-dependant tactile illusion over the dorsum of the hand where a PSE equal to 0.73 was detected by Longo & Haggard. Conversely, by increasing the long axis of the feed-forward synapses or by avoiding lateral inhibition, PSE within the second layer becomes as high as 0.93. This suggests the neuronal network could reproduce the very modest orientation-dependent tactile illusion over the palm. In fact, this part of the body presents a PSE, which is close to 1 (0.93 the value reported by Green; 0.96 the value reported by Longo). Different values of PSE as concern the dorsum and the palm suggest differences in rescaling effects. The neuronal network provides a greater rescaling on the palm.

The implemented model could be useful for a better understanding of the neural mechanisms underlying tactile distance perception and the orientation-dependent tactile illusion. Moreover it could be used to predict new results, such as tactile illusion at body parts not investigated yet.

Finally, it might be of interest to integrate the present work with the work realized by Enrico Altini concerning the Weber’s illusion (that is the same physical distance appears different when applied on different body regions) with the intent to implement a unique neuronal network able to simulate these two different aspects of tactile illusion.

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