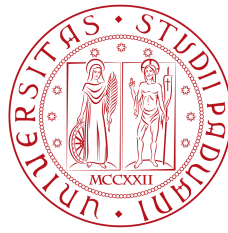


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Elaborato Finale

A variational approach to Perception and Psychophysics

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Riassunto

In questa tesi viene suggerita una possibile applicazione dei metodi del calcolo variazionale e della meccanica statistica alla costruzione di un modello della percezione in grado di collegare aspetti comportamentali e fenomeni di natura neurelettica.

Alla base del calcolo delle variazioni vi è infatti l'idea che l'evoluzione nel tempo di un sistema possa essere derivata come conseguenza di un principio di ottimizzazione applicato a qualche grandezza caratteristica. In particolare, dato un sistema che sta evolvendo da uno stato A a uno stato B, i metodi della meccanica analitica consentono di derivarne l'energia e il comportamento grazie a una funzione chiamata Lagrangiana. Infatti, tra tutti i possibili cammini che il sistema potrebbe seguire nel corso della sua evoluzione, la traiettoria reale sarà quella in grado di rendere stazionario un integrale della funzione Lagrangiana noto come Azione.

Pertanto, in questa tesi le variazioni nel tempo della sensazione saranno considerate alla stregua di cammini deducibili da un principio di ottimizzazione di cui verranno esplorate le implicazioni. Inoltre, l'energia necessaria a sostenere il processo stesso della sensazione verrà considerata come una misura della risposta neurelettica del sistema. In particolare, verrà esplorata una possibile relazione tra la sensazione e la risposta delle unità primarie afferenti.

Dopo una breve introduzione ai metodi matematici alla base della tesi, nel secondo capitolo verrà abbozzato un modello concettuale che consenta di applicare i metodi del calcolo variazionale alla percezione e alla psicofisica. L'idea alla base è dunque quella di considerare il cammino seguito dalla sensazione come se fosse la soluzione di un'equazione del moto derivabile nel contesto della meccanica analitica da un'equazione di Eulero-Lagrange. In aggiunta, l'energia posseduta dal moto stesso, sarà usata per caratterizzare il comportamento neurelettico del sistema.

Nel terzo capitolo tale modello verrà quindi formalizzato e applicato nel caso di stimoli costanti nel tempo. In particolare, per caratterizzare la traiettoria seguita dalla legge psicofisica nel tempo verrà utilizzato il fenomeno dell'adattamento psicofisico: una riduzione della sensazione provocata da una stimolazione costante può infatti essere considerata alla stregua di un moto da uno stato A a uno stato B. Verrà quindi derivata una funzione Lagrangiana, simile alla Lagrangiana di particella libera ma con una massa variabile, che risulterà al contempo una condizione sufficiente (ma non necessaria) per ricavare le fondamentali leggi della psicofisica, tenendo in considerazione anche eventuali caratteristiche di plasticità e la misurabilità delle variabili protetiche su scale a intervalli. Altre caratteristiche fondamentali del modello verranno poi investigate e collegate ad aspetti neurofisiologici: per esempio, la riduzione dell'energia durante il fenomeno dell'adattamento suggerisce un parallelismo con il comportamento del firing rate nelle unità primarie afferenti.

Nel quarto capitolo, quindi, i fenomeni neurelettrici verranno caratterizzati estendendo al dominio temporale la relazione di Naka-Rushton. In particolare, l'andamento del firing rate verrà caratterizzato tenendo conto dell'adattamento puro della frequenza di scarica e dell'adattamento del range percettivo. Il modello risultante, considerando l'energia come direttamente proporzionale al firing rate, consentirà di investigare il legame tra la risposta delle unità primarie afferenti e il corrispondente comportamento psicofisico: la sensazione risulta descritta da una relazione in grado di mutare da una legge di potenza a una logaritmica al variare del rapporto tra segnale e rumore; le variazioni della sensazione sono legate all'intensità del firing rate; l'adattamento psicofisico segue la dilatazione dell'intervallo tra gli spikes, e il sistema adatta minimizzando il numero totale dei potenziali d'azione.

Un test dei risultati preliminari verrà poi eseguito con dati presi dalla letteratura sul senso del tatto e mostra un buon accordo tra valori predetti e valori sperimentali, rinforzando l'idea che, nel senso del tatto, l'ipotesi di una connessione diretta tra la risposta delle unità primarie afferenti e la sensazione sia meno limitativa che in altri sensi. In particolare, la legge psicofisica e quella neurelettrica del modello rivelano gli stessi esponenti.

Nel quinto capitolo alcuni concetti di meccanica statistica verranno introdotti per inglobare nel modello due importanti caratteristiche: la risoluzione limitata dei sistemi psicofisici e la natura discreta di molte modalità sensoriali. In particolare, viene postulato che il sistema percettivo non sia in grado di discriminare tra sensazioni i cui correlati neurelettrici possiedano energie molto vicine tra loro. Partendo quindi da questa assunzione e sfruttando la forma dell'energia costruita nel capitolo quarto verranno ricavate alcune importanti leggi della psicofisica: la legge di Bloch e Charpentier (o di Weiss e Lopicque nel caso di stimolazione di tessuti), la legge di Ekman e un'espressione generale per la misura dei jnd, la relazione di Poulton e Teghtsoonian e infine una struttura della frazione di Weber in grado di descrivere sia il trend decrescente che caratterizza gli stimoli a bassa intensità, che la porzione crescente caratteristica dell'estremo superiore del range percettivo.

Quest'ultima relazione, in particolare, sarà testata su dati presi dalla letteratura e riguardanti la discriminazione della concentrazione di zucchero in una soluzione, la luminosità, il volume (sonoro), e la stimolazione della pelle, che rivelano un buon accordo ma evidenziano anche alcune difficoltà. In particolare, il minimo previsto dall'equazione anticipa sistematicamente quello dei dati, influenzando così la parte terminale della curva che tende a salire con una pendenza inferiore a quella reale.

Infine, nel sesto capitolo, il modello siluppato per stimoli costanti verrà esteso a stimoli variabili nel tempo e verrà fornita un'interpretazione preliminare dei risultati evidenziando alcune difficoltà e alcuni pregi del modello. Altri risultati o approfondimenti (come la derivazione delle legge di Pieron per i tempi di reazioni semplici a partire dall'entropia del modello) si trovano nelle Appendici.

Abstract

This thesis suggests an application of the methods of variational calculus and statistical mechanics to a possible model of perception capable of encompassing both behavioral and neuroelectrical phenomena.

The central idea of variational calculus is that the behavior of a system can be described as a consequence of an optimality request on some fundamental quantity. In particular, given a system evolving from a state A to a state B, the methods of analytical mechanics allow one to derive its energy and behavior by the knowledge of its Lagrangian function. Indeed, among all the possible patterns that the system could follow during its evolution, the natural one is the one which makes stationary an integral of the Lagrangian function called Action.

Thus, in this thesis, changes in sensation will be conceived as patterns in time, and the optimality constraint that they must satisfy will be investigated. Moreover, the energy needed to sustain sensation will be hypothesized to be related to the neuroelectric response. In particular, it will be mainly investigated a possible relation between sensation and the response of primary afferent units.

After a brief introduction on the mathematical methods needed in the treatise, in the second chapter will be sketched a possible theoretical framework that allows one to apply the concepts of variational calculus to perception and psychophysics. The general idea is to deal with the pattern followed in time by sensation as if it were a motion that can be derived in the context of analytical mechanics as a solution to an Euler-Lagrange equation. In addition, the energy possessed by the motion is posited to be, from a physiological perspective, related to the neuroelectric behavior of the system.

In the third chapter the model is then formalized and applied to a steady stimulus case. In particular, the psychophysical adaptation phenomenon will be chosen to describe the pattern followed by sensation in time. A depletion of the sensation elicited by a steady stimulus can indeed be seen as a motion from a state A to a state B. A possible Lagrangian function will be derived: a free particle Lagrangian, with a time-varying mass, that appears to be a sufficient (but not necessary) condition to derive the fundamental psychophysical laws while accounting for time-varying features and the measurability of prothetic continua on interval scales. Other fundamental features will then be investigated and tentatively connected with neurophysiological aspects. In particular, the depletion of energy during adaptation suggests a possible connection with neurophysiological aspects like the response of the firing rate in primary afferent units.

Hence, in the fourth chapter, a time-featured variation of the Naka-Rushton relation is introduced to characterize neuroelectric phenomena. In particular, the

pattern followed by the firing rate of primary afferent units is extended to time by the addition of pure spike frequency adaptation and dynamic range adaptation. The resulting model, when the energy is related to the firing rate, allows one to investigate a simplified model that links the response of primary afferent units to the corresponding psychophysical behavior. In particular, sensation appears to be described by an equation capable of switching from a power law to a logarithmic law depending on the signal-to-noise ratio. In addition, changes in sensation are driven by the firing rate, adaptation follows the increasing of the inter-spike-interval, and the system adapts minimizing the total number of action potentials.

A test of the preliminary results of the model reveals a good agreement with data taken from literature on the sense of touch, for which the approximation of a straight connection between sensation and the response of primary afferent units holds better than in the other senses. In particular, the psychophysical law and the neuroelectrical law of the model appear to have the same exponents.

In the fifth chapter some concepts of statistical mechanics are introduced to account for both the limited resolving power of the psychophysical systems and the discreteness of many sensory modalities. In particular, it will be posited that the perceiving system is incapable of discriminating between different sensations whose neuroelectric energies are very close to each other. Moving from this assumption and using the shape of the energy modeled in chapter four some laws of psychophysics will be derived: the Bloch-Charpentier law (or equivalently the Weiss-Lapicque law in the case of irritable tissues), the Ekman law and a general shape for the jnd, the Poulton-Teghtsoonian relation and finally a shape of the Weber fraction capable of accounting for both the decreasing trend at low intensities and the rising portion close to the end of the perceiving range.

The latter relation, in particular, will be tested on data taken from literature on the discrimination of sucrose concentration, heaviness, brightness, loudness and skin indentation, revealing a discrete agreement but also some shortcomings. In particular, its minimum appears to anticipate the actual one systematically, so that the rising portion increases more slowly than the actual data.

Finally, in the sixth chapter, the framework developed for steady stimuli will be extended to time-varying stimuli and a preliminary interpretation of the results will be given with a particular focus on some shortcomings and some strength points of the model. Other results or deepening on the model (like the derivation of Piéron's law for simple reaction time moving from the model's entropy) are given in the Appendixes.

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Introduction

The act of perceiving can be seen as a complex transduction of energy, ranging from a stimulus to its subjective representation, through receptors, nerve fibers, neural pathways and specialized regions of the brain. Nevertheless, although our knowledge of these processes is constantly growing, still an utter understanding of the topic is far from being achieved, leaving many questions unanswered.

A topic like perception, indeed, involves many levels of analysis, beginning from the low-level molecular, chemical and physiological features of sensory transduction and neuron's transmission, moving to the more entangled problem of network coding, ending up to the binding problem of how conscious perception and cognitive functions arise, or emerge, from all these interactions.

As a consequence, overlaps between several fields of science are common creating convergence among neuroscience, physiology and neurophysiology, chemistry, cognitive and computer science, biomedical engineering, psychology and mathematical psychology, physics, philosophy of mind, and so on.

Most of all, more than a century of researches has produced a massive plethora of results, empirical rules, theoretical issues and methodological approaches, often applicable only to specific domains, that have neither been encompassed in a unique framework nor derived by simpler general principles. Perhaps unification is an impossible goal to achieve, and surely perplexed by the complex, dissipative, and self-organizing nature of biological systems, yet it has always been an underpinning idea of scientific reasoning.

To understand the nature of the polytheism in brain and mind sciences, it is sufficient to highlight that, in the only domain of psychophysics, meant as the field of psychology that deals with the quantitative measure of sensation, the use of different assumptions, scaling techniques or sensory modalities leads to different results (for a review see Baird and Noma 1978, or Gescheider 1997).

A typical example is the psychophysical law, initially proposed in a logarithmic form by Fechner (1860), and subsequently challenged by Stevens (1956, 1957) that preferred a more flexible power law. Its nature has always been so debated that still there is no agreement as to its uniqueness and existence: while on one side classical methods, like constant stimuli, lead to a logarithmic law, on the other side magnitude estimation or cross-modality matching methods lead to a power law. Not to mention the differences in the psychophysical exponent that can be achieved by simply switching method (Baird and Noma 1978; Gescheider 1997).

Furthermore, standing on a more theoretical ground, Fechner's integration has been shown to hold only for certain shapes of Weber's law (Luce and Edwards 1958) and it has also been recognized that several possible and different laws of sensation

can be derived according to the scaling nature of the involved dependent and independent variables (Luce 1959). Moreover, in addition to the Weber-Fechner law and its more challenging rival, the Stevens power law, almost an infinite variety of different neuroelectrical laws have been shown to lead to a behavioral response that can be described by a power law (McKay 1963).

This situation is further entangled if we consider that, from an historical perspective (and with a broad approximation), psychophysical researches could be divided into two main streams, originated respectively from the inner and the outer psychophysics (Murray 1993).

Indeed, while on one side the study of the relation between stimulus and response (outer psychophysics) has led to the important results of Stevens' psychophysical law and scaling theory (Stevens 1956, 1957) and to the development of important foundational frameworks like measurement theory (Krantz et al. 1971; Falmagne 1985) or multidimensional Fechnerian scaling (Dzhafarov and Colonius 2001, 2005); on the other side, the study of the relation between neuroelectric phenomena and sensation (inner psychophysics) has led to a vast field of research ranging from signal detection theory (Green and Swets 1966; Egan 1975) to the application of Shannon's information theory to sensory systems (Norwich 1993; Norwich and Wong 1997; Luce 2003). In particular, researches in this latter field have led in the last century to an increase in the efforts of linking behavioral phenomena and neurophysiological correlates (for a review in visual neuroscience see Spillmann 2009) mostly due to the development of the functional brain-imaging techniques (for a review see Raichle 1998).

Moreover, the merging of psychophysical and neurophysiological studies has often aimed at investigating the relation between the response of primary afferent units and the sensation (Mountcastle et al. 1963; Stevens 1970). However, although this relation has been widely investigated, the linearity posited by sensory transduction theory (Stevens 1970), and by the neuron doctrine (Barlow 1972), is still argued: while several experiments seems to confirm it (Mountcastle et al. 1963; Borg et al. 1967; Johnson et al. 2002) several evidences of the contrary have also been found (see for a general review McKenna 1985; Krueger 1989).

It is straightforward to see that encompassing all these empirical evidences and theoretical results in a unique framework is a very tangled problem.

Nevertheless, although the mathematical methods in which are rooted Fechner's original ideas have been relevant in several works (Luce and Edwards 1958; Luce 1959; Krantz et al. 1971; Iverson 2006a,b), to our knowledge there has been no efforts to introduce the methods of variational calculus with the purpose of linking psychophysical and neurophysiological aspects.

Variational methods and minimum theories indeed plays a fundamental and unifying role in physics, chemistry, engineering, economics and biology (Schoemaker 1991). Besides, the paradigm of dynamical system theory, and related fields like analytical and statistical mechanics, have been recently applied to motor control (for a review see Engelbrecht 2001) and to cognitive sciences and psychology (see for instance Port and van Gelder 1995), where they have been both appreciated and criticized (Bechtel 1998). Furthermore, most of the neural networks approaches currently employed are based on statistical estimation, optimization, control theory, or energy (Borisjuk and Hoppensteadt 2004; Friston et al. 2006).

This thesis, then, suggests a possible application of the methods of variational calculus to neurophysiological and psychophysical topics, particularly focusing on Lagrangian and Hamiltonian mechanics as a main topic of dynamical system theory, in order to outline an abstract model of perception capable of encompassing both behavioral and neuroelectrical phenomena, starting from general principles and from the optimization of physical quantities, to describe sensation and the basic levels of perception with a focus on the energy of the process.

In analytical mechanics indeed, the energy of a system is described by means of the Hamiltonian function that is defined as the Legendre transformation of another function, the Lagrangian. The latter is a function summarizing the whole dynamics of a system and that allows one to derive the motion equations of a system evolving from a state A to a state B by the so-called principle of least action: the natural pattern is the one which makes stationary an integral of the Lagrangian function called Action.

The central idea of variational calculus is that the evolution of a system can be described as a consequence of an optimality request on some fundamental quantity. Thus, if sensation and perception were conceived as patterns in time, we could wonder whether they satisfy some optimality constraint. Moreover, in that case, would the energy of the system be supplied by metabolism? In other words, given a pattern describing the stimulus-response relation of an organism, is its Hamiltonian a measure of the energy supplied by metabolism in order to perceive?

The concept itself of an energy regulation underpinning perceptive phenomena can be traced back to the pioneer works of Helmholtz, Fechner and Herbart (see Murray 1993; Murray and Bandomir 2001), and like a common thread, it runs from the inner psychophysics' hypothesis of a relation between the subjective sensation and its neuronal substrate (Fechner 1860) to the neuronal noise in signal detection theory (Green and Swets 1966; Egan 1975) up to the later efforts to derive the laws of psychophysics moving from assumptions on neuroelectric phenomena (McKay 1963; Laming 1986; Norwich 1987, 1993). Moreover, while on one side the development of brain-imaging techniques allows one to perform correlational research with very high detail, on the other side is becoming possible to make an appraisal of the brain's energy consumption (Attwell and Laughlin 2001) and hence to measure the metabolic equivalent of perception (Schölvink et al. 2008).

For instance, recent studies seem to confirm that transient changes in metabolic brain's activity are related to variation in neuronal spiking frequency and in neurotransmitter flux: changes in oxygen consumption in the rat's brain are proportional both to the flux of excitatory amino acid glutamate, as measured by MRS, and to the change in the firing rate of a neuronal ensemble, as determined from extracellular recording (Hyder et al. 2002; Raichle and Gusnard 2002; Smith et al. 2002). Furthermore, electrophysiological studies on primates have shown that, in several senses, conscious perception is related to small local consumption of energy due to variations in the mean cortical neuron firing rate (Schölvink et al. 2008).

In this thesis we shall focus on a possible relation between an abstract model of sensation and the response of primary afferent units, in particular their firing rate. Nevertheless, the general idea could be generalized (in between certain boundaries) to the activity of populations of neurons in higher levels of cognition.

Finally, although the present framework in its general formulation would at-

tempt to deal with sensory systems that exhibit generalized time-varying features, to simplify the model we shall consider mainly the steady stimulus case. Moreover, since adaptive phenomena are often problematic, due to the existence of conflicting definitions of adaptation, habituation, fatigue, and stimulus failure (McBurney and Balaban 2009), adaptation will be meant as psychophysical adaptation when applied to a behavioral context, or as spike frequency adaptation and dynamic range adaptation when applied to a nerve fiber.

Contents of the chapters:

1. In the first chapter will be introduced the general mathematical methods needed in the treatise, with a particular attention to some fundamental concepts of Dynamical system theory (DST) and of Analytical mechanics (namely, the Lagrangian and the Hamiltonian functions that describe a system's behavior and its evolution in time). Some fundamental notions of variational calculus will be finally introduced. A lately useful example of a time-varying mass system and a description of the Naka-Rushton model (Naka and Rushton 1966) will be also given.
2. In the second chapter will be sketched a possible theoretical framework that allows one to apply the concepts of DST and variational calculus to the topics of sensation and perception, considering the psychophysical law and its evolution in time as the solution of an Euler-Lagrange equation. Two fundamental hypotheses will be given: first, the sensation and the subject's response are linearly dependent, constraining the system to very basic levels of perception; second, the energy that describes the sensation pattern is related to neurophysiological features.
3. In the third chapter the model will be formalized by applying it to a steady stimulus case. The main idea of treating sensation as a pattern in time is applied considering psychophysical adaptation as the only time varying phenomenon: a depletion of the sensation elicited by a steady stimulus can indeed be seen as a motion from a state A to a state B. The behavior of the psychophysical law during adaptation will be then considered as the solution of an Euler-Lagrange equation. A possible Lagrangian function will be derived: a free particle Lagrangian, with a time-varying mass, that appears to be a sufficient condition to derive the fundamental psychophysical laws while accounting for time-varying features and the measurability of prothetic continua on an interval scale. Other fundamental features will then be investigated and tentatively connected with neurophysiological aspects. In particular, the depletion of energy during adaptation suggests a possible connections with neurophysiological aspects. Furthermore, perception appears to be related to a cumulative process of energy and the adaptation phenomenon behaves like a negative feedback system on the energy previously accumulated. Some implications of hypothesizing a relation between the energy of the model and the metabolic consumption needed to sustain sensation will be analyzed.
4. In the fourth chapter a time-featured variation of the Naka-Rushton relation (Naka and Rushton 1966) will be introduced to characterize neurelectrical

phenomena. The resulting model, when the Hamiltonian is related to the spike frequency activity in a nerve fiber, allows one to investigate a simplified model of perception that links neuroelectrical features of primary afferent units and the corresponding psychophysical behavior. The results will be then compared to data taken from literature. Moreover, some fundamental but abstract quantities defined in chapter three will be explained in terms of physiological phenomena. In particular, the adaptation trend appears to be due to a minimization of the number of action potential released by the nerve. Furthermore, neuroelectrical and behavioral trends appear to follow different laws but with the same exponent.

5. In the fifth chapter other results of the model will be given: in particular, the fundamental laws of classical psychophysics, the Lapicque's law, the Bloch's law, the Poulton-Teghtsoonian's relation between psychophysical exponent and range of sensation, and a behavior of the Weber fraction that accounts for several discrepancies found in literature. Results are compared to data taken from literature.
6. In the sixth chapter the framework developed for steady stimuli will be extended to time-varying stimuli and a preliminary interpretation of the results is given with a particular focus on some shortcomings of the model. Several aspects that deserve further consideration will be also highlighted.
7. In the Appendixes have been collected several demonstrations and deepening of the model. In particular: an application of variational calculus to psychophysical laws in the space of stimuli; a biophysical model of nerve fiber that appears to be connected with the Lagrangian defined in the model; a link between the model's energy and Fisher's informational entropy; and the derivation of Pieron's law for simple reaction times moving from the model's entropy.

Chapter 1

Mathematical tools

This chapter contains a brief survey on Analytical Mechanics with a particular focus on Lagrangian and Hamiltonian systems. Some example is also given. In the last part the Naka-Rushton model is introduced. Since in the thesis the focus will be mainly on uni-dimensional system, the introduction is given for a single variable.

1.1 Motion equations

Let $q \equiv q(t)$ be a trajectory in a uni-dimensional space, with independent variable $t \in \mathbb{R}$. A classical example is the position of a point on a line describing a particle or the center of mass of an object moving in time, like in picture (1.1).

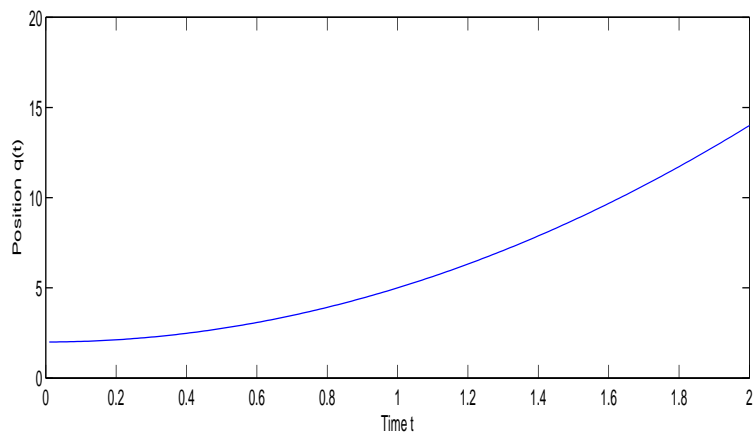


Figure 1.1: Point moving along the y-axis with trajectory $q(t) = 3t^2 + 2$.

More in general, a dynamical approach can be extended to any system evolving in time, like the current's flow in a circuit, the behavior of biological and economical systems, and so on. In other words, any quantity following a trajectory that can be approximated with a continuous variable described by some motion equation. Similarly, we could expect to describe with a motion equation the value of sensation ψ at the instant $t \in \mathbb{R}$, namely its position on the psychological continuum.

Let us consider now the simple case of a point moving along the axis \mathbb{R} . Once defined a trajectory $q(t)$, its velocity is given by its first derivative respect to time:

$$\dot{q}(t) = \frac{dq(t)}{dt} \equiv \lim_{\Delta t \rightarrow 0} \frac{q(t + \Delta t) - q(t)}{\Delta t} \quad (1.1)$$

that, graphically, corresponds to the inclination of the tangent to the trajectory. For instance, the tangent line to any point of the trajectory in picture (1.1).

Since the position q and the velocity \dot{q} characterize completely the state of a system that is evolving in time, the space of all the pairs (q, \dot{q}) is defined as the *state space* and is labeled as \mathcal{S} . Every trajectory $q(t)$ corresponds then to a unique graph in the state space and viceversa.

But, suppose we do not know the actual trajectory $q(t)$ followed by the system, nonetheless we know some general features of the system. Can we use this knowledge to characterize the behavior of a pattern without knowing its specific shape? In other words, can we build some general function in the state space \mathcal{S} , dependent on q, \dot{q} and maybe t , by which we can derive the final trajectory $q(t)$? This is exactly what analytical mechanics does by means of the Lagrangian and Hamiltonian functions, that are tightly related to the concept of energy.

1.1.1 Kinetic energy

The dynamical part of a system is described by the kinetic energy $T = T(\dot{q}, t)$. A quantity that, containing only the velocity \dot{q} , characterizes the amount of motion (or inertia) possessed by the system. For instance, in the most simple case is defined as a quadratic form like:

$$T = \frac{1}{2} c \dot{q}^2$$

where usually c is just a proportionality constant, namely $c \in \mathbb{R}$. For instance, in the case of a particle in motion it becomes its mass m (or its density ρ if we are working with some liquid system), that is:

$$T = \frac{1}{2} m \dot{q}^2 \quad (1.2)$$

The more an object is massive, or the more is fast, the more kinetic energy it possesses (and the more is difficult to stop it). Notice however that, in the most general case, kinetic energy could also be a function of time, $T(t)$, for instance:

$$T(\dot{q}(t), t) = \frac{1}{2} m(t) \dot{q}^2 \quad (1.3)$$

The previous equation can be imagined as describing a moving system that loses or increases its mass, for instance a balloon losing air or a bucket losing water¹.

¹Actually the problem of a time-varying mass system is more complicated, the previous wants to be just a naive example (see for instance Plastino and Muzzio 1992; Leubner and Krumm 1990; Flores et al. 2003)

1.1.2 Potential energy

At the same time the system could be impinged by some external force, possessing then a further contribute to energy due to the environment in which the motion is set. This second term is usually described by the potential energy that depends on the position in the trajectory, namely $U = U(q)$. Typical examples are the gravitational and electromagnetical fields in physics. Nevertheless, in a general treatise it could be any effect or constraint acting upon the system and could be dependent also on velocity, or time itself.

Suppose now we have a potential term $U(q)$ affecting a motion that otherwise would be related to the only kinetic part $T(\dot{q})$. We need to consider both these terms to describe the behavior of the system. For instance we could write the following expressions:

$$L = T(\dot{q}) - U(q) \quad , \quad H = T(\dot{q}) + U(q)$$

where in the first one we have subtracted the contribute of the potential energy to the kinetic one, while in the second one they have been summated. As we will see these two functions are respectively called the Lagrangian and the Hamiltonian of a system. It is straightforward to understand that, while the Lagrangian is a difference of energies, the Hamiltonian is a sum. In particular, then, the Hamiltonian is a measure of the total energy possessed by a system.

A very typical example is an object of mass m attached to a spring with an elastic constant k . In this case the potential energy of the system can be written as $U(q) = \frac{1}{2}kq^2$ and corresponds to the work done by the recalling force of the coil acting on the mass. Since the spring acts on the mass perturbing its free motion its potential energy must be added to the system. Hence:

$$L = \frac{1}{2}m\dot{q}^2 - \frac{1}{2}kq^2 \quad , \quad H = \frac{1}{2}m\dot{q}^2 + \frac{1}{2}kq^2$$

The most important result of analytical mechanics is that, starting from a Lagrangian the trajectory $q(t)$ can be derived by means of an equation.

1.1.3 Lagrangian and Euler-Lagrange's equation

More in general, it can be shown that any trajectory $q(t)$, given its kinetic and potential energies, can be found as the result of an Euler-Lagrange's equation:

$$\frac{d}{dt} \left(\frac{\partial L}{\partial \dot{q}} \right) - \frac{\partial L}{\partial q} = 0 \tag{1.4}$$

where the function $L = L(q, \dot{q}, t)$ is exactly the Lagrangian. It is however important to notice that a structure of the Lagrangian like $L = T - U$ is generally not needed. Lagrangian, indeed, can be any function like $L(q, \dot{q}, t)$. *Natural lagrangian systems* are those that satisfy a decomposition in kinetic and potential parts, instead *generalized Lagrangian systems* are those in which the dependence of the function on the trajectory and the velocity can be any function.

Generally, the Euler-Lagrange equation corresponds to a second order differential equation whose solution is the trajectory followed by the system. A derivation of equation (1.4) will be given later in the context of variational calculus, since it is very useful to understand the philosophy underlying the methodology.

The importance of the Lagrangian function is in the fact that, once that it is known, the application of the Euler-Lagrange equation (1.4) gives as a result the motion equation $q(t)$. Furthermore, as we will see, the Lagrangian function L is related to energy, given by the Hamiltonian function H , with a simple coordinate's transformation called the Legendre transformation.

A simple example of how the motion equation can be derived by the Euler-Lagrange equation is given by an object moving with kinetic energy (1.2), without any force acting on it, hence $L = T$, and we have:

$$\frac{d}{dt} \frac{\partial (\frac{1}{2}m\dot{q}^2)}{\partial \dot{q}} = \frac{d}{dt}(m\dot{q}) = 0 \rightarrow \ddot{q}(t) = 0 \rightarrow q(t) = \dot{q}(0)t$$

That is, an object free from the influence of external forces moves of a uniform motion with constant velocity.

Adding now a potential term corresponding to the presence of a spring, the Euler-Lagrange equation gives:

$$\ddot{q}(t) = -\frac{k}{m}q(t) \rightarrow q = A\cos(\sqrt{\frac{k}{m}}t)$$

that is generally known as the solution of the harmonic oscillator. Namely, an object attached to a spring (without friction) oscillates.

1.1.4 Properties of invariance

Euler-Lagrange's equation and Lagrangian functions possess interesting properties of invariance.

1. Lagrange's equations are shape-invariant to changes in the coordinate's system. Taking indeed a regular and invertible transformation (namely, a local diffeomorphism) like $(q, \dot{q}) \rightarrow (\tilde{q}, \dot{\tilde{q}})$, Lagrangian can be rewritten as:

$$\tilde{L}(\tilde{q}, \dot{\tilde{q}}, t) = L(q(\tilde{q}, t), \dot{q}(\tilde{q}, \dot{\tilde{q}}, t), t)$$

and it can be shown that, while $q(t)$ is the solution of equation (1.4), the new trajectory $\tilde{q}(t)$ is the solution of:

$$\frac{d}{dt} \left(\frac{\partial \tilde{L}}{\partial \dot{\tilde{q}}} \right) - \frac{\partial \tilde{L}}{\partial \tilde{q}} = 0$$

Hence the shape of Euler-Lagrange's equation is the same under coordinate's transformation.

2. Different Lagrangian functions can have the same motion equation $q(t)$ as solution to their Euler-Lagrange's equations. For instance, the addition of a constant or of a multiplicative factor to L does not change the shape of the solution. More in general, given a function $F(q, t)$ and a real constant $c \neq 0$, the two different Lagrangians $L(q, \dot{q}, t)$ and

$$L'(q, \dot{q}, t) = cL(q, \dot{q}, t) + \frac{dF}{dt}(q, \dot{q}, t)$$

give the same motion equations. Namely, Lagrangians that differ from each other only for a function that is a total derivative of time are equivalent. This last property is also known as gauge's invariance.

1.2 Hamiltonian

The Lagrangian approach to the dynamic of a system is a very powerful methodology since, once known the Lagrangian function L , it allows one to derive the whole behavior of the system. Nonetheless, the predictive power of the framework can be further increased by switching to the Hamiltonian formalism. Hamiltonian function H is indeed what is usually considered the energy of the system.

Hamilton's equations and the Hamiltonian function can be straightly derived from Lagrangian once defined the variable conjugate momentum:

$$p(q, \dot{q}, t) \equiv \frac{\partial L}{\partial \dot{q}} \quad (1.5)$$

Indeed, the Hamiltonian function is defined as the Legendre transformation of the Lagrangian function:

$$H(p, q, t) = [p(q, \dot{q}, t) \cdot \dot{q} - L(q, \dot{q}, t)]_{\dot{q}=\dot{q}(p, q, t)} \quad (1.6)$$

with the condition that the Hessian matrix (in our case the second derivative respect to the velocity) of $L(q, \dot{q}, t)$ has to be different from zero.

Hamilton's equations instead, similarly to the Euler-Lagrange equation in the Lagrangian formalism, allow to obtain the motion of the system:

$$\dot{q} = \frac{\partial H}{\partial p} \quad , \quad \dot{p} = -\frac{\partial H}{\partial q}$$

whose solutions describe the trajectories followed by the variables $q(t)$ and $p(t)$.

For a natural lagrangian system, in which $L = T - U$, and the kinetic energy has a shape like (1.2) it is straightforward to see that the Hamiltonian takes the form $H = T + U$ as we have previously seen. In the particular case of *natural lagrangian systems*, then, the total energy is the sum of both the kinetic energy and of the potential energy. It is also straightforward to see that, with the only kinetic part defined by (1.2), namely in the absence of external influences on the system,

Lagrangian and Hamiltonian are exactly the same $L = T = H$ and Hamilton's equations become:

$$\dot{q} = \frac{\partial T}{\partial p}, \quad \dot{p} = 0$$

the second one in particular states that the momentum p does not change during the motion, hence is a conserved quantity. This is a result that will be useful later.

Hamiltonian then, to sum up, is the total energy of the system and its dependence on time can be obtained as:

$$\dot{H}(q, p, t) = \frac{\partial H}{\partial t} = -\frac{\partial L}{\partial t}$$

If the Hamiltonian (and the Lagrangian) changes in time we have a dissipative (or non-conservative) system, otherwise the system is conservative, since the value $H = E$ is a constant during all the motion $q(t)$. In the particular case of a conservative natural system, $E = T + U$, hence during the motion there's an exchange of energy between the kinetic and potential term but the sum is always equal to E . Non-conservativity instead implies that the energy dissipates or is exchanged with the environment as if the system were not close or isolated.

A very simple example of energy is the free particle case, in which $p = m\dot{q}$ and hence the Lagrangian gives the Hamiltonian:

$$H = \frac{p^2}{2m}$$

Since the Hamiltonian does not depend on time the value of the energy will be the same during the whole motion.

In the case of a potential $U(q)$ we will have instead:

$$H = \frac{p^2}{2m} + U(q)$$

For instance, let us consider an elastic force:

$$H = \frac{1}{2}m\dot{q}^2 + \frac{1}{2}kq^2$$

In this case the energy is the sum of the kinetic energy, describing the amount of motion of the mass m , and a potential term describing the effect of the recalling force of the spring. When the mass slows down is because the force of the coil is increasing, and viceversa, since the energy is conserved.

1.2.1 Some considerations on spaces

In the Lagrangian formalism the *state space* has been defined as the space \mathcal{S} of all the points (q, \dot{q}) . Instead using Hamiltonian formalism we can define the *phase space*, namely the space Γ of all the points (q, p) .

These two sets of variables are both useful to give an insight into the system's nature and, most of all, are equivalent: the switch between the Lagrangian and the Hamiltonian formalism can always be done if the momentum (1.5) is invertible. Such a requirement is locally satisfied if the second derivative of the Lagrangian is not zero, namely $\frac{\partial^2 L}{\partial \dot{q}^2} \neq 0$. A good sufficient global condition instead is that L be a convex function of \dot{q} .

It is also worthy to notice that the Hamiltonian in the phase space is invariant for regular and reversible transformations of the local coordinates system as like Lagrangian is in the state space. Besides, in the phase space there exists also a wide set of coordinate's transformation, known as canonical transformations, that mix up more deeply configurational coordinates and conjugate momenta. In general then the Hamiltonian description of energy is considered a more powerful instrument than the Lagrangian's.

1.3 Noether's Theorem

Energy E is one of the so-called integrals of motion that are related to the symmetries of a system and to conservation laws. For instance, as we have seen before, if Hamiltonian and Lagrangian are time independent we have the energy conservation law: hence energy is a consequence of the homogeneity of time.

This idea has been generalized by Emmy Noether in a very important theorem.

Noether's Theorem states that, given a parameter $\alpha \in \mathbb{R}$, and a family of local diffeomorphisms like:

$$\begin{aligned} q &\rightarrow \varphi(\alpha, q) \text{ such that } \varphi(0, q) = q \\ \dot{q} &\rightarrow \psi(\alpha, q, \dot{q}) = \frac{\partial \varphi}{\partial q} \dot{q} \end{aligned}$$

If for every choice of q, \dot{q}, α we have:

$$L(\varphi(\alpha, q), \psi(\alpha, q, \dot{q}), t) = L(q, \dot{q}, t)$$

hence the quantity (with p defined in (1.5)):

$$C(q, \dot{q}, t) = \frac{\partial \varphi}{\partial \alpha}(0, q) p(q, \dot{q})$$

is an integral of motion for L , that is, $C(q, \dot{q}, t)$ is invariant during all the motion of the system and keeps a constant value. Namely, the quantity C is conserved.

The general idea is the system possesses some symmetry (and hence the Lagrangian is invariant under its specific coordinate's transformation) there is some quantity that is conserved during the motion. Famous examples are the conservation of momentum p , that relies on the invariance of Lagrangian for translations in space (homogeneity of space), and the conservation of angular momentum that relies on rotational invariance (isotropy of space).

1.4 Variational Formulation

A natural framework for the Euler-Lagrange equation is the Variational calculus, a very important field of mathematics that deals with optimization problems. The solutions of this class of problems (in this case the motion of the system) can indeed be seen as a consequence of an optimality constraint over some mathematical structure called functional. In other words, given all the possible patterns followed by a system the actual one is the one which makes stationary some quantity mathematically built in the form of a functional.

Formally, a functional is a map over a vector space that returns elements of a scalar field. Broadly speaking, a functional F is a law or application that, applied to a function f gives a real number, i.e., the resulting $F[f]$ belongs to \mathbb{R} .

For instance, a simple duality principle states that, given a function:

$$f : x \rightarrow f(x)$$

that associates the value $f(x)$ to the variable x , it is straightforward to define a functional as:

$$F : f \rightarrow f(x)$$

that instead associates to every function f the value $f(x)$ that the function attains at a specific point x .

Since we are interested in optimizing a functional we must know how it varies by changing the function f . Yet, while it is intuitive that the derivative of a function f respect to its independent variable x is given by $\dot{f}(x) \equiv \frac{df(x)}{dx}$, as defined by (1.1), what happens when we look for the derivative of F respect to a function f ?

The notion of functional variation is similar to the definition of a directional derivative for a function: given a variation δf of the function f related to some parameter², for instance $f_\alpha = f + \alpha\delta f$, the Gateaux differentiability is:

$$\delta F[f, \delta f] \equiv \left. \frac{d}{d\alpha} F[f + \alpha\delta f] \right|_{\alpha=0} \quad (1.7)$$

Let us consider now a function $f(x)$ defined over the dominion $\mathcal{T} = [a, b]$ for $a, b \in \mathbb{R}$, and considering a functional with a shape like:

$$F[f] = \int_a^b L(f(x), \dot{f}(x), x) dx \quad (1.8)$$

where L is some regular function of the function f , its derivative \dot{f} , and the independent variable time. In Analytical mechanics, where the independent variable x is the time t , and the function f is the position q , the function L is exactly the Lagrangian, and the functional F is called the Action.

²This results can be also generalized to any family of functions $f_\alpha(x)$ that are not necessarily linearly related to α .

We can now calculate its variation (see for instance Landau and Lifshitz 1960):

$$\delta F[f] = \left(\frac{\partial L}{\partial \dot{f}} \delta f \right) \Big|_a^b - \int_a^b \left(\frac{d}{dx} \frac{\partial L}{\partial \dot{f}} - \frac{\partial L}{\partial f} \right) \delta f \, dx \quad (1.9)$$

In particular, if we consider the case in which the extremes of the pattern are fixed, that is $\delta f(a) = \delta f(b) = 0$, we obtain that the functional F is stationary, $\delta F = 0$, only if the Euler-Lagrange equation is satisfied:

$$\frac{d}{dx} \left(\frac{\partial L}{\partial \dot{f}} \right) - \frac{\partial L}{\partial f} = 0 \quad (1.10)$$

the particular solution f of the previous equation, often called a *geodetic*, is also the solution of the optimization problem modeled using the functional $F[\psi]$.

1.5 Variable mass

An example that will be particularly useful later is a particle with a variable mass. Several physical systems possess variable masses like any vehicle burning oil, or a bucket with a hole, or a rocket in space burning its fuel.

Let us imagine, for instance, an object of mass m that depends on the temperature T of the room, that is $m(T)$. Its kinetic energy is:

$$H = \frac{p^2}{2m(T)} \quad , \quad L = \frac{1}{2}m(T)\dot{q}^2$$

with momentum equal to $p = m(T)\dot{q}$. Keeping the room at a constant temperature the object behaves like a free particle of mass m following a uniform motion. Hence, given an initial thrust (initial energy and momentum), its velocity is a constant depending only on the temperature in the room $v = p/m(T)$.

But what happens if the temperature in the room changes in time?

Let us imagine that the mass increases if the temperature increases. Hence there is a function describing the temperature, $T(t)$, that implies a dependence of the mass on time $m(T(t))$. Hence, the kinetic energy is (let us write $m(t)$ instead of $m(T(t))$ for sake of simplicity):

$$H = \frac{p^2}{2m(t)} \quad , \quad L = \frac{1}{2}m(t)\dot{q}^2$$

It follows from Euler-Lagrange's equation that the momentum $p = m(t)\dot{q}$, given by the initial thrust, is conserved. Hence, if the object's mass increases its velocity decreases and the motion is not uniform. The Euler-Lagrange equation implies:

$$\ddot{q} = -\frac{\dot{m}}{m(t)}\dot{q} \quad \rightarrow \quad q(t) = \int \frac{p}{m(t)} dt$$

The pattern followed depends on the changes in the room's temperature (notice that if the temperature is kept constant we have the free particle's uniform motion).

Moreover, in contrast to momentum, the energy is not conserved: kinetic energy indeed decreases if the object's mass increases. This behavior can be approximately explained as follows: an initial thrust is given to the object that starts moving with momentum p and energy $E(0) = \frac{p^2}{2m(0)}$. Then, since there are no external forces acting on it, its momentum is conserved during the whole motion. However, as the temperature increases in the room, the object becomes gradually massive. But the momentum is constant so the object has to decelerate. Hence the kinetic energy decreases until the body stops being too massive.

The Hamiltonian is then time dependent and the system is dissipative. This non-conservativity can be seen as a sort of external influence on the system. Notice however that such an influence is not due to some external force since there are no potential terms like $U(q)$. It should be considered more a feature of the system, that changes adjusting itself to the environmental condition, without being affected by some external force.

Finally, it is important to stress that this example of dynamic mass is very naive and formally debatable in several points (see for instance Plastino and Muzzio 1992; Leubner and Krumm 1990; Flores et al. 2003). Yet it is very useful to give a general understanding of the dissipativity of the system with variable mass since the same Lagrangian will be later used to describe perception.

1.6 The Naka-Rushton model

A widespread behavior in neuroelectrical phenomena is a monotonic increase, as the stimulus intensity raises, until the system reaches a saturation, like in picture (1.2). A similar behavior ranges indeed from the kinetics of many enzymes to the responses of a quite number of sensory transduction processes and neurons impinged by a steady stimulus.

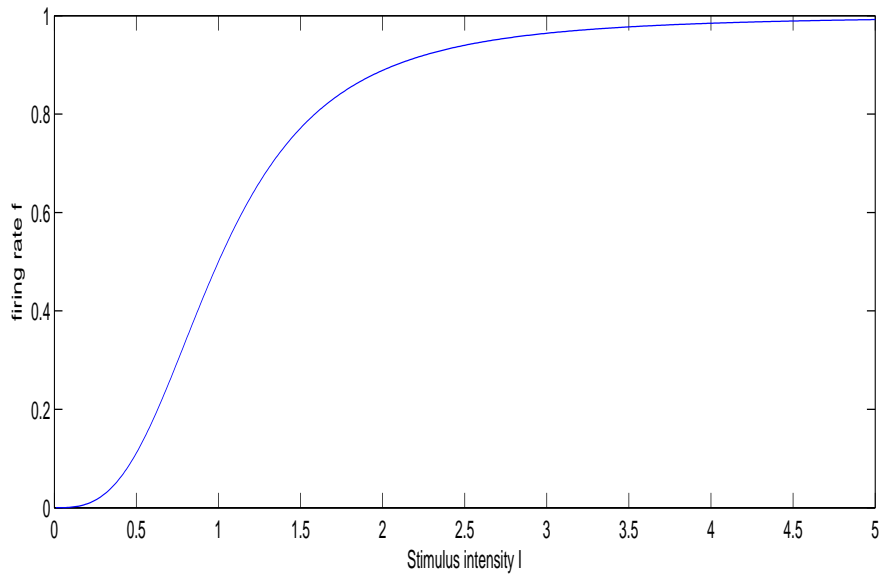


Figure 1.2: Naka Rushton model for $n = 3$, $f_{Max} = 1$, $\sigma = 1$.

Among the sigmoidal or logistic models often used to shape this firing rate's behavior, one of the most important and widely applied is the Michaelis-Menten model or Naka-Rushton relation (Naka and Rushton 1966), also known as rectangular hyperbolic function or log tanh relation.

Generally his shape is written as:

$$f = f_{Max} \frac{I^n}{\sigma^n + I^n} \quad (1.11)$$

In the limit of $I \rightarrow \infty$, when the stimulus intensity reaches high values, the firing rate saturates to the value f_{Max} . The intensity σ instead is the one at which the firing rate takes half of its maximum value, $f(\sigma) = f_{Max}/2$, moreover it can be considered a measure of the dynamic range of the nerve fiber: the bigger the value of σ , the broader the range in which the firing rate does not saturate.

As a case of study, in the following chapters, the Naka-Rushton relation will be used to describe the electrical activity of a nerve fiber, thus leading to a relation between the psychophysical law and the neuroelectrical behavior. It is worth of notice that, while the framework developed in the next chapters is completely general, both the choices of a nerve fiber and of a precise shape of the energy as we will do are just particular cases. Different choices will indeed lead to different results and behavior of the system.

Chapter 2

On a general framework

In this chapter will be introduced the ideas underlying a possible analytical framework. In the first section it will be suggested how dynamical system theory could be used to describe sensation and perception, allowing one to consider the temporal features of a system. Then, in the second section, a general structure will be developed in order to apply variational calculus. In particular it will be detailed a possible interpretation of the formalism that leads to consider the Hamiltonian as a measure of the neuroelectrical activity underpinning perception.

2.1 General features

Despite the discrete nature of the world, perception appears to be a rather continuous phenomenon. From a physical and chemical point of view our senses deal with a discrete reality that are able to grasp with very high resolution: smell and taste works at the same level of molecules and atoms; vision receptors can detect single quanta of lights; the sense of hearing, although it does not work at quantal level, still at the eardrum level is capable of appreciating fluctuations of an atom's width (Torre et al. 1995; Gescheider 1997). Yet our perception of the world is, at a certain degree, smooth, continuous, to such an extent that thought itself seems to be rather continuous.

Besides, when we perceive, hear, even think, from a certain point of view we *use* functions. A truly general definition of function does not exist, for it depends on the branch of mathematics in which we are: sometimes a function is defined by a graph, sometimes by the expressed dependence between two quantities, generally is considered a rule that associates some element of a set to one or more elements of another set. Nevertheless, the intuitive concept of function is very simple: a rule that describes how something changes.

Functions are indeed abstractions of processes and, at a certain degree, the process of perception could be schematized as a composition of functions: intensity is firstly transformed at the receptor potential level, then it's coded in the firing rate of the primary afferent units, and so on, through neural pathways and specialized regions of the brain, until is reached the final step. Response itself is often seen in this perspective: the heaviness is a function of the weight of an object one has just grabbed.

In between all these steps there must be a sort of transition between discreteness and continuousness, since the final resolution is too coarse-grained to appreciate differences of the order of some atom. In other words, the Weber fraction is not capable of appreciating an infinitesimally small difference in the intensity of the stimulus. This suggests, on one side, that a general framework should encompass the discrete nature of the world (not to mention the discreteness inherent to the firing rate coding); on the other side, it suggests the idea of working with continuous functions, at least to a first degree of approximation, to shape both sensation and the final response of the organism. While the idea of a discretization will be introduced later in the treatise (see chapters four and five), the rest of this chapter and the next one will mainly deal with the introduction of a continuous framework.

2.1.1 A dynamical approach

The main idea underlying the introduction of a dynamical approach is to enclose the temporal features of a system to describe its evolution (Port and van Gelder 1995). For instance, the inner representation of a time-changing event could be at the origin of some observed systematic tendencies of the observers in misjudging the actual events. A typical example of such a topic is the representational momentum, namely the observers tendency to extend an event beyond its actual ending point (see for a review Thornton and Hubbard 2002).

Similar phenomena are indeed common in naive physics or in experiments on causal perception (see for instance McKay 1963; Twardy and Bingham 2002), where subjects exhibit several wrong beliefs on the motion of a point, of a pendulum, of the trajectory followed by objects falling down (see for instance Bozzi 1990). More in general, similar effects can be identified also out of the vision domain, like in the illusory duration of ramped and damped sounds (Schlauch et al. 2001; Grassi and Darwin 2006).

These phenomena could be described, at least from a qualitative point of view, by a psychophysical law that exhibits perceptual acceleration or movements that are not present in the actual stimuli. Representational momentum itself might be related to something similar: a law of motion different from the actual one could imply a misjudging of velocity and acceleration that yield to a misplacement of the ending point. Obviously, this is a strong simplification of a very complex phenomenon that does not involve only the evaluation of acceleration, velocity and direction of motion, but also of the object's weight, of the friction, of any information, expectation or belief about the trajectory, of several aspects and features of the physical surroundings and of the length of the retention interval between the event and the probe (Thornton and Hubbard 2002). Nevertheless, since we are interested in an abstract and highly reductive model of the evolution of perception in time, a dynamical approach seems to be the natural starting point.

As an example: be $I(t) = tI_B + (1 - t)I_A$, for $t \in [0, 1]$, a linearly varying loudness stimulus that spans all the values between the intensities I_A and I_B , at a constant velocity $\dot{I} = I_B - I_A$. If $I_B > I_A$ we have a ramped stimulus, viceversa if $I_B < I_A$ we have a damped stimulus.

In a very naive model, considering that perception of loudness is described by the Fechner's law, $\psi = k \log I$, showing a logarithmic compression, we could take

for the time dependence simply $\psi(t) = k \log I(t)$, thus:

$$\dot{\psi}(t) = \frac{k(I_B - I_A)}{I_B t + (1 - t)I_A}$$

Now, what happens if we assume that the previous equation is in some way related to the perceived rate of change in the stimulus?

It is simple to show¹ that the logarithmic compression implies for a ramping stimulus a decrease in velocity as if there was a deceleration, whereas for a damping stimulus leads to an increase in velocity as if there was an acceleration. As a consequence the ramping stimulus is perceived as decelerating while the damping stimulus is perceived as accelerating.

An inner equivalent of inertia, like in the representational momentum, might lead to state that a ramping stimulus is expected to vanish before than the corresponding damping stimulus. Indeed, it has been empirically found (see for instance Schlauch et al. 2001) that ramped tones (gradual attack and abrupt decay) are perceived as shorter than damped tones (abrupt attack and gradual decay).

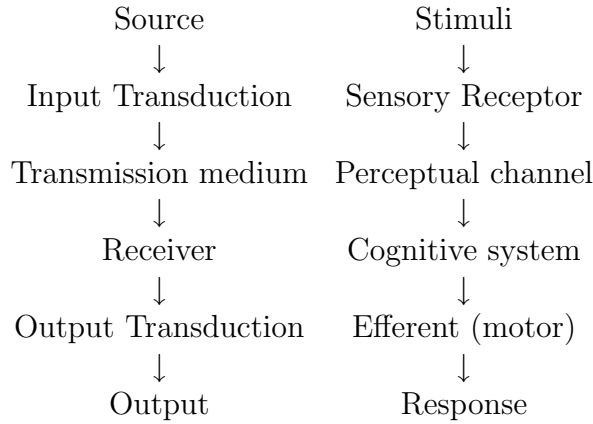
Obviously, the previous example does not claim to be a complete description of the actual phenomenon. On the contrary, it is a quite naive argument. Notwithstanding this, it is useful to introduce dynamical system as a framework for describing perceptual events allowing to derive their behavior from abstract and fundamental principles. From now on we will then describe psychophysical law ψ and the subject's response R using continuous functions.

Hence, in this thesis, the focus will be mainly on intensity-type stimuli, like the number of decibels of a sound, the concentration of an odorant in the air or of a solute in a solution, the intensity of light, the weight of an object, the indentation of skin, and so on. These kind of stimuli are considered to arise corresponding prothetic psychological continua, like auditory loudness, taste sensation, visual brightness and lightness, numerosness, duration, heaviness, apparent length, and so on. These are, in a broad sense, psychological scales corresponding to quantitative aspects of sensation. On the other hand, metathetic attributes are defined as those that account for more qualitative features of stimuli, like visual position and contour, auditory pitch, inclination, proportion, and so forth. The idea underpinning prothetic continua is an addition of excitation to excitation moving along the relative continuum, for metathetic continua is instead a substitution of excitation for excitation (Stevens and Galanter 1957; Stevens 1957). Since we are interested in trying to shape a continuous analytical treatise, prothetic continua appear to be more suitable candidates; hence the main focus will be more on a quantitative metric of sensation. Yet it must be kept in mind that metathetic continua are often tightly connected with continuous physical quantities.

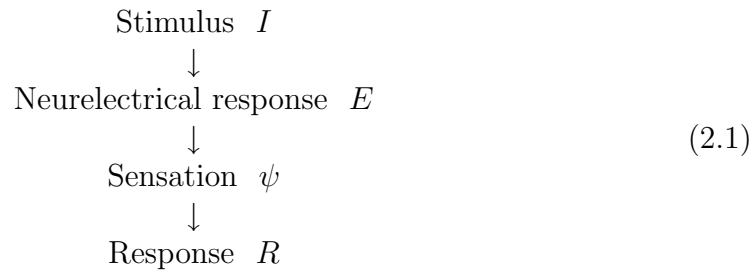
¹For a ramped stimulus ($I_A = 60\text{dB}$, $I_B = 80\text{dB}$) we have $\dot{\psi} > 0$ since perception is increasing, in particular: $\dot{\psi}(0) = k/3$ and $\dot{\psi}(1) = k/4$, hence is decelerating. For a damping stimulus ($I_A = 80\text{dB}$, $I_B = 60\text{dB}$) instead we have that $\dot{\psi} < 0$ since perception is decreasing, but it takes the values $\dot{\psi}(0) = -k/4$ and $\dot{\psi}(1) = -k/3$, hence is accelerating.

2.1.2 Diagrams of perception

A widely used simplification of a general parallelism between a communication system and a cognitive system follows the schema (Baird and Noma 1978):



In particular, a slight variation of this pattern for a single perceptual channel is the so-called psychophysical chain that moves from a stimulus, through its neuroelectrical representation, sensation and eventually response (Murray 1993):



It must be stressed, however, that a similar psychophysical chain implies a strong assumption of independence between different stimuli and perceiving processes. Such an assumption is not completely true, since at the levels of amygdala and orbitofrontal cortex most of the pathways of sensation converge in the so-called associative memory systems (Rolls and Deco 2010). Hence, considering that in the first steps after the receptors's transduction, all the senses possess unimodal systems and can be considered like independent channels of perception², a possible diagram describing the psychophysical chain should be:

$$\begin{array}{ccccccc}
 I_1 & \rightarrow & E_1 & \rightarrow & \psi_1 & \searrow & \\
 \dots & \rightarrow & \dots & \rightarrow & \dots & \rightarrow & R(\dots, \psi_k, \dot{\psi}_k, \dots, t) \\
 I_n & \rightarrow & E_n & \rightarrow & \psi_n & \nearrow &
 \end{array} \tag{2.2}$$

where different stimuli I_1, I_2, \dots, I_n are detected by separated processes, transformed into neuroelectrical responses E_1, E_2, \dots, E_n , corresponding to sensations

²For instance, visual stimuli are processed by the V1, V2, V4 areas of the brain and then by the inferior temporal cortex; taste stimuli follow the nucleus of the solitary tract, then the thalamus VPMpc nucleus and then frontal operculum and insula and primary taste cortex; olfactory stimuli instead run through the olfactory bulb and the olfactory (pyriform) cortex; touch instead reaches the thalamus VPL and then the primary somatosensory cortex (Rolls and Deco 2010).

$\psi_1, \psi_2, \dots, \psi_n$, and hence elaborated and processed to give a perceptual response R that, in general, could be any function of the psychophysical laws ψ_k and their derivatives. Notice that there are no hypothesis on the existence or on the shape of the psychophysical law, for different systems might obey to different laws.

It is interesting to stress, in the previous diagram, that any further process performed on sensation ψ could be seen as a composition of functions. For instance, most of the psychophysical measurements, like in magnitude estimation methods, are carried by associating a rank, a category, or a number to the sensation (Baird and Noma 1978; Gescheider 1997). Indeed, not only the use of function of functions and functionals in psychophysics and mathematical psychology is not a novelty (see for instance Krantz et al. 1971), but also similar diagrams are widespread used in experimental psychology and economics, like in integration information theory (Anderson 1981) or multi-attribute evaluation models (Oral and Kettani 1989) and Sensory Science, like in classical models of sensory input, integration by CNS and motor output (Baird and Noma 1978).

Nevertheless, for what concern this thesis we will focus on the behavior of a single abstract channel as depicted by the simplified diagram (2.1). In particular, in order to further simplify it we will rely on an hypothesis of linearity between the sensation and the subject's response.

2.1.3 Linearity assumption

A typical assumption that is commonly made in psychophysics (see for instance Anderson 1981) is that the subject's final response is proportional to the sensation. This is often called the linearity assumption:

$$R = a\psi + b \text{ for } a, b \in \mathbb{R} \quad (2.3)$$

For instance, a particularly widespread methodology used in multi-attribute evaluation models, like those of conjoint analysis (Luce and Tuckey 1964) or of functional measurement (Anderson 1981), consists in a decomposition of the subject's response into a sum of attributes that are often interpreted as subjective measure of the importance of the attribute itself. As an example, information integration theory states that there are three fundamental cognitive laws: additive, multiplicative and averaging. These three laws can be considered subclasses of diagrams (2.1) and (2.2). Taking indeed:

$$R : (\psi_1, \psi_2) \rightarrow \mathbb{R}^+ , R = a\psi_1 + b\psi_2 + c\psi_1\psi_2 + d$$

in the general case of $a, b, c, d \neq 0$ we have a simple regression model like those used in conjoint analysis. When $a = b = 0$ the model is multiplicative. When $c = 0$ the model is additive. If $c = 0$ and $a + b = 1$ we have instead an averaging model. The term d is often used to account for initial conditions (Anderson 1981).

Following this linearity hypothesis the psychophysical chain (2.1) can be reduced to the study of the relation between:

$$\begin{array}{ccc}
\text{Stimulus } I & & \\
\downarrow & & \\
\text{Neuroelectrical response } E & & (2.4) \\
\downarrow & & \\
\text{Sensation } \psi & &
\end{array}$$

In particular in the following chapters we will focus on a possible relation between these quantities based on some optimality constraint.

2.2 On a general model

Following the previous considerations we have reduced the psychophysical chain to the elements of stimulus, neuroelectrical response and sensation. To shape a relation between these three we will use variational calculus. A detailed formalization of the theory will be given in chapter three.

2.2.1 Hypothesis on Lagrangian and perception

Many problems in several field of science are based on optimization of functionals (Schoemaker 1991). For instance, all the physical systems follow as a natural rule the law that makes stationary a functional like (1.8).

If we take as a stimulus some physical phenomenon, like some object moving, rotating, crashing, oscillating, we can write down a Lagrangian that summarizes the motion. The resulting equations, once that boundary or starting conditions are set, can be used to describe the evolution of the system.

Why something similar couldn't happen in our mind? Could it be possible that we possess, or create as an heuristic, some Lagrangians (or Hamiltonians) for what we perceive and sense? Why couldn't we consider sensation or perception as patterns that makes stationary some functional?

Anybody indeed has expectations and beliefs about physical phenomena, beliefs that could be considered deterministic and mechanistic from several point of views. Moreover, as we have highlighted before, naive physics studies have shown several stereotypical wrong beliefs and tendencies in misjudging the actual motion (see for instance Bozzi 1990; Schlauch et al. 2001; Grassi and Darwin 2006; McKay 1963; Twardy and Bingham 2002).

There could be a Lagrangian description for our expectations and beliefs. Perhaps, something built with experience, or reasoning, or intuition. Such a Lagrangian might describe a correct, or misjudged, motion and obviously could depend on different quantities than those contained in the actual physical Lagrangian.

In particular, during the first milliseconds of perception, where the answer of the system is highly mechanistic and still unaffected by higher cognitive functions, one could expect that sensory systems obey to some physiologically codified and deterministic pattern. Under this perspective it sounds sensible that sensation (and maybe perception) could emerge from variational laws.

As an example, of all the possible patterns that the phenomenon of psychophysical adaptation could follow, why a particular perceptual channel choose often the

same one? Why this particular pattern couldn't be the one minimizing a specific functional $F[\psi]$? Following the ideas of variational calculus then, the motion of psychophysical law during time would be the solution of an Euler-Lagrange equation associated to a functional $F[\psi]$.

More in general, since any kind of pattern can be obtained by a Lagrangian, independently on its nature, one could expect that any element of the psychophysical chain (2.4) could be derived by a Lagrangian:

$$\begin{array}{ccc} I & \leftarrow & L_I \\ \downarrow & & \\ E & \leftarrow & L_E \\ \downarrow & & \\ \psi & \leftarrow & L_\psi \end{array} \quad (2.5)$$

Notice that we have chosen not to write any relation between the Lagrangians, because, in the most general case, they could be totally independent and detached. Besides, at the present moment, Lagrangians are just abstract descriptions of the pattern followed by any quantity. In particular, the previous diagram implies for the Legendre transformation (1.6) a similar result for the Hamiltonians:

$$\begin{array}{ccc} I & \leftarrow & H_I \\ \downarrow & & \\ E & \leftarrow & H_E \\ \downarrow & & \\ \psi & \leftarrow & H_\psi \end{array} \quad (2.6)$$

Nevertheless, of all the quantities listed in diagrams (2.5) and (2.6), since we are interested in analyzing perception, our focus will be just on the Lagrangian and the Hamiltonian that summarize the behavior of sensation, namely:

$$L_\psi : \psi \rightarrow L(\psi, \dot{\psi}, t) \quad \text{and} \quad H_\psi : \psi \rightarrow H\left(\psi, \frac{\partial L}{\partial \dot{\psi}}, t\right) \quad (2.7)$$

that are related to the functional:

$$F : \psi \rightarrow F[\psi] = \int_{t_0}^{t_R} L(\psi, \dot{\psi}, t) dt \quad (2.8)$$

defined between the onset t_0 and the offset t_R of the stimulus.

Recalling now that a functional is a function that takes other functions as its arguments and gives as a result a scalar number, the functional F will return, for a given L (and hence H), a numerical value that changes by changing the pattern ψ . Different patterns followed by sensation will then be labeled by this functional, the natural one being the one that makes stationary the functional. Such a stationarity could be for instance the result of a compromise between survival aspects and energetical issues: the lowest necessary value to perceive and react, within a sensible time, yet without wasting too much metabolic energy.

In particular, since the Hamiltonian describes the energy of the process, and at the same time is the energy needed to maintain it, we could wonder if it should also describe (or at least be related) to the energy that must be supplied by metabolism. In that case, since sensation is based on the neuroelectric activity, one could expect the Hamiltonian to be related to the neuroelectric response E .

This fundamental hypothesis can be schematized as follows:

$$\begin{array}{ccc}
 I & & \\
 \downarrow & & \\
 E & \approx & H_\psi \\
 \downarrow & \swarrow & \\
 \psi & &
 \end{array} \tag{2.9}$$

and will be further discussed in chapter three and used in chapter four to connect sensation to the response of primary afferent units. Briefly, we expect the neuroelectric response to be a function of the stimulus intensity and to be equivalent to the Hamiltonian describing the pattern followed by sensation.

2.2.2 Possible approaches

From a general perspective, we could consider two different approaches to diagram (2.9). The first one is exemplified in a Lagrangian like:

$$L(\psi, \dot{\psi}, t) \quad \text{where} \quad \dot{\psi} = \frac{\partial \psi}{\partial I} \dot{I} + \frac{\partial \psi}{\partial t} \tag{2.10}$$

or in the case of a steady stimulus:

$$L(\psi, \dot{\psi}, t) \quad \text{where} \quad \dot{\psi} = \frac{\partial \psi}{\partial t} \tag{2.11}$$

A different approach can be obtained by neglecting the time dependence:

$$L(\psi, \psi', I) \quad \text{where} \quad \psi' = \frac{d\psi}{dI} \tag{2.12}$$

Notice that, in this second approach, the psychophysical law is like a field on the space of the stimuli since the independent variable becomes I . The formalism is the same, it is only needed to make the substitution $I \rightarrow t$. Yet the results are expected to be different. Nonetheless, in the following chapters will be considered only the first case, but some details on the second case are given in Appendix A.

2.2.3 Psychophysical law and Noether's theorem

Independently on the chosen approach, if one considers a transformation of the psychophysical law, then, using the Noether's theorem outlined in section (1.3), if the Lagrangian remains the same there's a quantity C that is an integral of motion, namely, a quantity that is invariant during the motion of the psychophysical law

in time. The viceversa is also interesting: if we have some properties or symmetries that we need to be possessed by the system we can take the correspondent transformations of the psychophysical law and see which features are needed in the Lagrangian to satisfy them.

For instance, a fundamental property of prothetic continua is that they are measured on an interval scale. Hence their correspondent admissible transformation is an affine transformation (Luce 1959; Krantz et al. 1971). Given then:

$$\varphi(\psi, \alpha) = \psi + \alpha \quad \text{with } \alpha \in \mathbb{R}$$

Noether's theorem assures that (see next chapter for a detailed proof) for the system to be invariant for translations, the Lagrangian must be independent on ψ . That is, the Lagrangian is symmetric under the changes in the value of sensation, hence it has general shape:

$$L \equiv L(\dot{\psi}, t) \tag{2.13}$$

and the conjugate momentum:

$$\Pi \equiv \frac{\partial L}{\partial \dot{\psi}} \tag{2.14}$$

is conserved quantity during the motion. It is also interesting to notice that this property agrees with the idea, detailed in section (2.1.1), that prothetic continua are conceived as an addition of excitation to excitation, like a sort of additivity of sensation.

2.3 Summary

In this chapter a possible general framework has been introduced suggesting that dynamical system theory and variational calculus could be applied to perception and psychophysics. The general idea is to deal with the pattern followed in time by sensation as if it were a motion equation that can be derived in the context of analytical mechanics as a solution to an Euler-Lagrange equation. In that case, indeed, among all the possible patterns that sensation could follow the chosen and natural one would be the one making stationary a functional associated to the Lagrangian of the system. In addition, the Hamiltonian of the system can be derived as a Legendre's transform of the Lagrangian. Hamiltonian is the function related to the energy possessed by the motion, hence, from a physiological perspective, it could be the energy supplied by metabolism in order to sustain the process of sensation. The fundamental hypothesis then, is that the Hamiltonian function is related to the neuroelectrical behavior of the system.

Chapter 3

A variational approach to sensation

In this chapter will be formally built the model sketched in the previous chapter. Once defined a shape of the Lagrangian that allows to account for both classical psychophysical laws and time-varying features, the properties of the system will be analyzed and detailed in the case of the psychophysical adaptation phenomenon. As a result, psychological prothetic continua appear to be measured on an interval scale, energy decreases during adaptation resembling the behavior of the firing rate in nerve fiber, and the sensation results to be an accumulation of energy, similarly to the way jnds are usually accumulated in psychophysics.

3.1 Preliminary Hypotheses

In order to simplify as much as possible the calculations and the general interpretation of the equations, some assumptions are needed:

1. The stimulus I will be a steady one and hence constant in time.
2. The only time-varying feature of perception will be the psychophysical adaptation phenomenon and it will be considered to deplete to extinction.
3. The time dominion of the adaptation will be the interval $\mathcal{T} \equiv [t_0, \infty]$ between the onset t_0 of the stimulus and the total adaptation at $t \rightarrow \infty$.

3.2 Definition of psychophysical law

Let $I \in \mathbb{R}^+$ be a stimulus intensity. From a general point of view, given a time dominion \mathcal{T} between its onset and its offset, a stimulus can be defined as a function $I : \mathcal{T} \rightarrow \mathbb{R}^+$, while a psychophysical law can be defined as a function of both stimulus intensity and time:

$$\psi \equiv \psi(I(t), t) \tag{3.1}$$

Notice that a direct dependency on time is needed to account for time-varying features like the psychophysical adaptation phenomenon: given a steady stimulus, $I(t) \equiv I \forall t \in \mathcal{T}$, only a psychophysical function that directly depends on time allows for further variation of perception ψ . Indeed, considering a time-varying intensity stimulus we can immediately define the first derivative respect to time of the psychophysical law as:

$$\dot{\psi}(I(t), t) \equiv \frac{\partial \psi}{\partial I} \dot{I} + \frac{\partial \psi}{\partial t} \quad (3.2)$$

The first partial derivative describes the actual velocity at which perception is changing when the stimulus change, while the second partial derivative is a measure of the rate at which perception is changing in time (notice that in general the previous equation is not necessarily a measure of the perceived velocity). It is immediate to notice that if we are considering a steady stimulus situation, namely $I(t) \equiv I \in \mathbb{R}^+$ for all $t \in \mathcal{T}$ so that $\dot{I}(t) = 0$, equation (3.2) then becomes:

$$\dot{\psi}(I, t) = \frac{\partial \psi}{\partial t} \quad (3.3)$$

hence any variation of the psychophysical law does not depend on the stimulus but only on its time-varying features, like adaptive or plastic phenomena.

Psychophysical law can then be represented, in the general case, as a trajectory in time $\psi : \mathcal{T} \rightarrow \mathbb{R}^+$, while in the steady stimulus case $\psi(I, t)$ can be seen as a family of patterns described by the parameter $I \in \mathbb{R}^+$ and with independent variable $t \in \mathcal{T}$. Besides, as we have seen in the first chapter, it corresponds to a graph in the state space $\mathcal{S} \equiv (\psi, \dot{\psi})$ where each point summarizes the intensity of the sensation and the rate at which sensation is changing in time.

3.3 Application of variational calculus

From an analytical mechanical perspective, the pattern $\psi(I, t)$ followed by the psychophysical law during the adaptation phenomenon can be considered the solution of an Euler-Lagrange equation.

Hence, considering the framework of variational calculus introduced in section (1.4), it exists a functional $F[\psi]$ (i.e., a function that takes other functions as its arguments and gives a scalar as a result) that is stationary for the function $\psi(I, t)$ or, in other words, it attains a maximum or a minimum value exactly for a certain shape of $\psi(I, t)$. The extremality condition is then formally obtained requiring that the variations of the functional $F[\psi]$, induced by variations $\delta\psi$ in the psychophysical law, are equal to zero:

$$\delta F[\psi] = F[\psi + \delta\psi] - F[\psi] = 0 \quad (3.4)$$

and implies a differential equation whose solution is exactly $\psi(I, t)$. In particular, since we are interested in functionals that has the form of an Action:

$$F[\psi] = \int_{\mathcal{T}} L(\psi, \dot{\psi}, t) dt \quad (3.5)$$

when the variation of the function ψ is negligible at the extremes of the interval \mathcal{T} , (namely $\delta\psi(t_0) = \delta\psi(\infty) = 0$ as it is in the case of psychophysical adaptation), the variational condition is equivalent (see for instance Landau & Lifshitz, 1960) to the Euler-Lagrange equation:

$$\frac{d}{dt} \left(\frac{\partial L}{\partial \dot{\psi}} \right) - \frac{\partial L}{\partial \psi} = 0 \quad (3.6)$$

Briefly, the previous equations state that, of all the possible pattern that adaptation can follow, between the values $\psi(I, t_0)$ and $\psi(I, \infty)$, the natural pattern is the one that satisfies the extremality condition (3.4) on the functional (3.5) and hence is the solution of the equation (3.6).

Given then the Lagrangian for sensation, the variable conjugate momentum can be introduced as in definition (1.5):

$$\Pi \equiv \frac{\partial L}{\partial \dot{\psi}} \quad (3.7)$$

and the behavior of the system, in addition to the previously introduced state space \mathcal{S} , can be described also in the phase space $\Gamma \equiv (\psi, \Pi)$ where, as like in (1.6), Legendre's transformation defines the Hamiltonian as:

$$\mathcal{H}(\psi, \Pi, t) \equiv \left[\Pi \dot{\psi} - L(\psi, \dot{\psi}, t) \right]_{\dot{\psi}(\psi, \Pi, t)} \quad (3.8)$$

It must be recalled that the two sets of variables $(\psi, \dot{\psi})$ and (ψ, Π) are both useful to give an insight into the system's nature and, most of all, are equivalent: indeed the switch between the Lagrangian and the Hamiltonian formalism can always be done if the momentum (3.7) is invertible. Such a requirement is locally satisfied if the second derivative of the Lagrangian is not zero, namely $\frac{\partial^2 L}{\partial \dot{\psi}^2} \neq 0$. A good sufficient global condition instead is that L be a convex function of $\dot{\psi}$.

Finally, it must be stressed that, following the formalism of analytical mechanics, the quantities Π and \mathcal{H} have been also defined as the *momentum* and the *energy* related to the *motion* of the system in time. Nevertheless, at the present moment they are still a rather abstract description of the system's behavior. To understand their meanings in the context of adaptation a Lagrangian $L(\psi, \dot{\psi}, t)$ that returns the psychophysical law as the solution of equation (3.6) is needed.

3.4 A shape for the Lagrangian

As we have already noticed in chapter one, in the very general case Lagrangian could be a rather complicated function of its arguments, thus belonging to the *Generalized Lagrangian Systems*.

Nonetheless, a very simple class of Lagrangian appears to be a sufficient condition (see Appendix B) to derive the fundamental laws of psychophysics while accounting for time-varying features, namely:

$$L(\dot{\psi}, t; I) = \frac{1}{2} m(I, t) \dot{\psi}^2 \quad (3.9)$$

where the notation $L(\dot{\psi}, t; I)$ states that the Lagrangian is a function of $\dot{\psi}$ and t , while I is just a parameter. In addition, the quantity $m(I, t) \neq 0$ acts like a modulating function that depends both on stimulus intensity and time and allows the transformation (1.5) to be invertible. Equation (3.9) depicts the process of adaptation as a free particle motion with a variable mass like in the model shown in section (1.5). Hence the inertia of the system can increase or decrease depending on its dependencies on time and stimulus intensity.

Due to its particular shape, the strongest objection that could be raised to Lagrangian (3.9), is that it has already its solution built into it. Indeed, once one has set the function $m(I, t)$ the solution ψ will be univocally determined. Hence any function ψ could be derived with an appropriate choice of $m(I, t)$. The answer to this objection is not a simple one: first of all, it is important to emphasize that Lagrangian (3.9) is just one out of an infinite possible number of functions that, with a variational approach, describe different systems. Second, it is a sufficient but not a necessary condition, because it is not the only Lagrangian that gives the classical psychophysical laws as solution of an Euler-Lagrange equation¹. Third, a structure of the Lagrangian like $L(\dot{\psi}, t)$ is required by the Noether's theorem to ensure the measurability of the psychophysical quantities on an interval scale, see section (3.1.5); hence, using a quadratical shape is just choosing the simplest possible, yet meaningful, Lagrangian. Fourth, but not less important, the fact that a Lagrangian like (3.9) can give any function once opportunely set-up does not imply that its particular shape could not be used by some physical system.

Notwithstanding this, equation (3.9) has been chosen because, although its structure and the idea of a system's inertia depending on time and on stimulus intensity may somewhat sound factitious, it exhibits several interesting features that are proper of the process of perception. Besides, it takes a very simple meaning in the case of a primary afferent unit as we will see in chapter four.

As an immediate result, it is worthy of notice that a similar shape of the Lagrangian suggests the idea that, if the modulating function $m(I, t)$ were related to some physiological features, the entire process of sensation would be somehow layered over other processes. Indeed, in such a case different sensations, based on different neurophysiological processes or sensory modalities, would always be driven by the same abstract rule in spite of their different nature.

Other interesting properties are related to the solutions of Lagrangian (3.9) and to the momentum and the energy.

¹For instance, as it has been already pointed out in the first chapter, the motion equations are invariant for gauge's transformation, that is: a Lagrangian L' that differs from L only for a function that is a total derivative of time, $L_0 = \frac{dF}{dt}$, gives the same motion equations. Other possible Lagrangians are also given in Appendix B.

3.5 The psychophysical laws

The Euler-Lagrange equation (3.6) that corresponds to Lagrangian (3.9) is:

$$\ddot{\psi} = -\frac{\dot{m}(I, t)}{m(I, t)} \dot{\psi} \quad (3.10)$$

Psychophysical laws are then its solutions:

$$\psi = c_1 \int \frac{1}{m(I, t)} dt + c_2 \quad (3.11)$$

with constants $c_1, c_2 \in \mathbb{R}$.

Different choices of $m(I, t)$ lead then to different psychophysical laws but they all obey to the abstract behavior depicted by Lagrangian (3.9) and equation (3.10). Fechner's and Stevens' laws, for instance, appear to be (see Appendix B) solutions of the same differential equation in two different limits: Fechner's solution holds in the limit of small psychophysical exponent, $n \rightarrow 0$, where the Stevens' law becomes a trivial constant (Krueger 1989).

As it has been noticed in the previous section, sensation ψ would then be univocally determined by a specific choice of $m(I, t)$, as if it were a process based on other processes: different psychophysical laws could be possible but they all would obey the abstract behavior depicted by Lagrangian (3.9), irrespective of how the system encodes information. If the function $m(I, t)$ were related to neurophysiological features a Lagrangian like (3.9) would be a common abstract rule that connects different trends of perception to the ongoing physiological processes.

3.6 The conjugate momentum

Following definition (3.7) the conjugate momentum for the system depicted by Lagrangian (3.9) is defined as:

$$\Pi = m(I, t)\dot{\psi} \quad (3.12)$$

and, in the case of the adaptation phenomenon, it behaves like a compound measure of the rate at which the system is adapting and of its inertia.

Besides, being the Lagrangian (3.9) independent on the magnitude of psychophysical law ψ , the momentum is conserved during the motion:

$$\frac{d\Pi}{dt} = \frac{d}{dt} \frac{\partial L}{\partial \dot{\psi}} = \frac{d}{dt} (m(I, t)\dot{\psi}) = 0$$

Noether's theorem, stated in section (1.3), indeed implies that the system is invariant under translations. Fitted to the present case the theorem states that given a transformation of the psychophysical law:

$$\psi \rightarrow \varphi(\psi, \alpha) \quad \text{such that} \quad \varphi(\psi, 0) = \psi$$

if the Lagrangian is invariant, namely:

$$L(\phi, \dot{\phi}, t) = L(\psi, \dot{\psi}, t)$$

hence the quantity:

$$C = \frac{\partial \varphi}{\partial \alpha} \frac{\partial L}{\partial \dot{\psi}}$$

is a constant during the motion.

It is straightforward to verify that for $\varphi(\psi, \alpha) = \psi + \alpha$ the conserved quantity is exactly $C = \Pi$ since:

$$C = \frac{\partial(\psi + \alpha)}{\partial \alpha} \frac{\partial L}{\partial \dot{\psi}} = m(I, t) \dot{\psi} = \Pi$$

Hence, an affine transformation of the psychophysical law $\varphi(\psi, \alpha) = \psi + \alpha$ leaves the system unchanged: as a consequence, ψ is measured on an interval scale meeting a fundamental measurement requirement for prothetic continua and for several classes of psychophysical laws (Luce 1959; Krantz et al. 1971).

It is also interesting to notice that the admissible transformation related to a ratio scale, namely $\varphi = \alpha\phi$, neither fulfills the requirement of Noether's theorem nor leaves unchanged the Lagrangian, since $L_\psi = L_\varphi\alpha^2$. Yet it is still interesting that it simply implies a scaling of the Lagrangian (and hence of the Hamiltonian) as if we were only changing the unit of measure.

Furthermore, the phase space Γ becomes very useful to describe the system's behavior since adaptation of different sensory modalities is expected to assume different values of Π . In addition, the conservation of momentum implies that changes in perception are inversely related to $m(I, t)$. Hence, during the adaptation, as $\dot{\psi}$ decreases in time, m increases like an expanding mass or growing inertia. Looking at the picture from a reversed perspective: if m were related to some physiological aspect, then its increasing would imply a decreasing in the rate of adaptation. For instance, in the fourth chapter, applied to a simplified model of nerve fiber, $m(I, t)$ will be related to the inter-spike interval (ISI), while conservation of Π will indicate that the signal propagates with constant velocity within the nerve.

Finally, since $\dot{\psi}$ during psychophysical adaptation is a monotonic negative function, Π is assumed to be negative in order to have $m > 0$. However, in the general case of a time-varying stimulus, $\dot{\psi}$ could be a non monotonic function, hence the conservation of momentum will allow $m(I(t), t)$ to take both positive and negative values. Anyway, the transformation (3.7) is always globally invertible if $m \neq 0$.

3.7 Hamiltonian

The Hamiltonian can be found by means of Legendre's transformation (3.8), in the phase space Γ , where it takes the form:

$$\mathcal{H}(\Pi, t; I) = \frac{\Pi^2}{2m(I, t)} \quad (3.13)$$

Due to the constancy of Π the system's energy can be seen as an inverse measure of the inertia $m(I, t)$, or equivalently a direct measure of the change in perception:

$$\mathcal{H}(\dot{\psi}, t; I) = \frac{\Pi}{2}\dot{\psi} \quad (3.14)$$

It also appears to be related to the way the system encodes information as if it were an *internal representation* of the stimulus: indeed, if $m(I, t)$ is a one-to-one relation for $I \in \mathbb{R}^+$, different stimulus intensities will elicit different values of the energy. Hence, as it has been hypothesized in section (2.2.1), if the Hamiltonian were a measure of the neuroelectrical response E , it would be exactly a function of the stimulus intensity $E(I)$, independently on the magnitude of sensation.

3.7.1 Variation of the Hamiltonian

The system generally belongs to the family of the non-autonomous Hamiltonian systems, being time dependent:

$$\frac{d\mathcal{H}}{dt} = -\frac{1}{2} \left(\frac{\Pi}{m(I, t)} \right)^2 \dot{m}(I, t)$$

Energy is generally not conserved during the motion and the system is dissipative. The only conservative case occurs indeed for a time independent value of $m(I, t) \equiv m(I) \forall t \in \mathcal{T}$ at which the psychophysical law (3.11) takes the form $\psi = \frac{c_1 t}{m(I)} + c_2$. So the system is conservative only if sensation increases linearly with time. Such a psychophysical law is empirically false in the case of a steady stimulus if the time dependence describes only the adaptation phenomenon.

Moreover, it is interesting that the previous expression can be rewritten as:

$$\frac{d\mathcal{H}}{dt} = \frac{\Pi}{2}\ddot{\psi}$$

that curiously resembles the Newton's law. That is, if the hypothesis stated in section (2.2.1) were true and the Hamiltonian were a measure of the neuroelectric activity, the previous equation would state that variations in the neuroelectric activity correspond to acceleration in the variation of sensation.

Finally, during psychophysical adaptation, when $m(I, t)$ increases, energy must decrease. In particular, considering a finite variation we have:

$$\frac{\Delta\mathcal{H}}{\mathcal{H}} = -\frac{\Delta m}{m}$$

that is, a relative decrease in the value of the modulating function m corresponds to a relative increase in the Hamiltonian.

This suggests a parallelism with neurophysiological features: for instance, adaptation in nerve fibers is related to a decrease in electrical activity (Galambos and Davis 1943; Torre et al. 1995; Wen et al. 2009). More generally, a depletion of the energy supplied by the organism means a reduction in its costs. Transient changes in metabolic brain's activity are indeed related to variation in neuronal spiking frequency and in neurotransmitter flux: changes in oxygen in the rat's brain are proportional both to the flux of excitatory amino acid glutamate, as measured by MRS, and to the change in the firing rate of a neuronal ensemble, as determined from extracellular recording (Attwell and Laughlin 2001; Hyder et al. 2002; Raichle and Gusnard 2002; Smith et al. 2002). If, as it has been suggested in section (2.2.1), this energy has to be supplied by metabolism, the Hamiltonian could be related to some detectable measure of energy like the firing rate of a primary afferent unit, or the level of activity of a neuronal ensemble. This parallelism, indeed, developed in the fourth chapter with the application of the model to a nerve fiber, will lead to consider the energy to be a measure of the electrical spiking activity. As a results the modulating function $m(I, t)$ will appear to be related to the inter-spike interval (ISI) while the conservation of the momentum Π will be related to the constant velocity of the impulses' propagation within the nerve fiber.

3.7.2 Hamiltonian and Perception

Experimental results seem to suggest that particular magnitudes of activity are needed to support neural functions (Raichle and Gusnard 2002). Indeed, both the changes in oxygen consumption and in mean spike frequency in neuronal ensembles, needed to reach a stimulated level, are greater starting from lower baselines artificially induced by different levels of anesthesia. This suggests the existence of an overall activity that must be fulfilled to activate brain processes. Furthermore, the maximum levels of metabolic oxigen consumption and mean firing rate that can be achieved during the stimulation are the same starting from different baselines (Hyder et al. 2002; Smith et al. 2002).

An application of these concepts to the Hamiltonian permits one to account for energy differences between a value \mathcal{H}_S , corresponding to the stimulated level, and a value \mathcal{H}_0 corresponding to the baseline resting activity. In the case of an Hamiltonian like (3.13), that behaves like a function of both stimulus intensity and time, $\mathcal{H} \equiv \mathcal{H}(I, t)$, the minimum value \mathcal{H}_0 related to the spontaneous activity, could be taken as corresponding to the energy elicited by the threshold stimulus I_0 . Its value, $\mathcal{H}_0 \equiv \mathcal{H}(I_0, t)$ could be considered the threshold for perception. The energy actually involved in sensation should then be decreased by the effect of this absolute threshold:

$$\mathcal{H}_P(I, t) = \mathcal{H}_S(I, t) - \mathcal{H}_0 \quad (3.15)$$

In a general framework energy $\mathcal{H}_S(I, t)$ could be related to the effective consumption sustained by the organism in order to trigger a process, while energy (3.15) could be the part devoted to sensation.

Thus, in the general case, the psychophysical law (3.11) could be rewritten as:

$$\psi = c_1 \int \mathcal{H}_P(I, t) dt + c_2 \quad (3.16)$$

with constants $c_1, c_2 \in \mathbb{R}$. Sensation then appears to be the result of accumulating the internal energy, similar to the way jnds are usually accumulated in psychophysics. Moreover, the functional associated to sensation results to be, in a given time interval $[t_0, t_1]$:

$$F[\psi] = \int_{t_0}^{t_1} \frac{\Pi}{2} \dot{\psi} dt = \frac{\Pi}{2} [\psi(I, t_1) - \psi(I, t_0)] \quad (3.17)$$

that is, the functional is a measure of the variations in the psychological continuum. The quantity that we are asking to be stationary is then the variation itself of sensation. Indeed, the variational condition (3.4) becomes equivalent to:

$$\delta F = 0 \rightarrow \delta(\psi(I, t_1) - \psi(I, t_0)) = 0 \quad (3.18)$$

Such a requirement states that the variations along the subjective scale must be stationary (in this particular case, since the Legendre condition $\frac{\partial^2 L}{\partial \psi^2} = m$ is greater than zero, the extremum is a minimum). Hence, between two instants of time (likely the onset and the offset of the steady stimulus), this ideal system is adapting making the minimum possible variation in sensation.

Finally, the previous equation, in the specific case of the adaptation phenomenon, can be written as:

$$\psi(I, t) = \psi(I, t_0) - \frac{2}{|\Pi|} \int_{t_0}^t \mathcal{H}_P(I, \tau) d\tau \quad (3.19)$$

Hence the sensation, at any moment $t \in \mathcal{T}$, can be seen as a reduction of the initial value (accumulated during the rising phase) at the onset of the stimulus, as if energy were taken away at this time. Equation (3.19) can indeed be seen as the response $r(t) = s(t) - f(t)$ of a simple inhibitory feedback system with input signal $s(t) \equiv \psi(I, t_0)$ and suppressor integrator $f(t) = \int \mathcal{H}_P(t) dt$. A similar behavior has been used to characterize adaptation in neural systems (Drew and Abbott 2006). Inhibitory feedback has also been used to characterize adaptation in sensory neurons relating the increasing in the absolute refractory period to the activity of ionic currents (Fohlmeister 1979; Gerstner and Kistler 2002).

3.8 On the linearity assumption (2.3)

It is interesting to see that the shape of the Lagrangian (3.9) in the steady stimulus case is tightly related to the linearity assumption (2.3) between the response and the psychophysical law. This lead to an interesting interpretation.

In the steady stimulus case perception $\psi(I, t)$ is a family of pattern in time, parametrized by the stimulus intensity I . Hence we have, between the time of the onset of the stimulus $t = t_0$ and a time $t = t_1$:

$$I \rightarrow \psi \rightarrow F[\psi] = \int_{t_0}^{t_1} L(\psi, \dot{\psi}, t) dt \quad (3.20)$$

We could interpret the time-dependent behavior of ψ as if the system, impinged by the steady stimulus, adapted itself in order to tune the perception. Nevertheless, we could expect the functional F to be independent from time but not from the stimulus intensity's value. Indeed, as we have seen in the previous section, the functional associated to the Lagrangian (3.9) is:

$$F[\psi] = \frac{\Pi}{2} [\psi(I, t_1) - \psi(I, t_0)] \quad (3.21)$$

Hence we have a family of functionals, $F(I) = F_I[\psi]$, dependent on the parameter $I \in \mathcal{I}$, since the integration cancels any dependence on the time but not on the stimulus intensity that is just a parameter.

This behavior is very similar to a stimulus-response pattern $R(I)$, and most of all, with the choice of Lagrangian (3.9), the functional $F[\psi]$ is linearly dependent on the sensation ψ and hence closely related to the linearity assumption (2.3) between R and ψ , unless of some scaling term.

In the general case, however, the result of the functional $F[\psi]$ could be completely detached from the linearity assumption (2.3). For instance it is straightforward to verify that, keeping time constant, a trivial choice like:

$$F[\psi] = (\psi^{-1}(\psi(I)))^n \rightarrow F(I) = I^n$$

gives as observed response a power law independently on the psychophysical law that underpins the act of perception. The previous equation is similar to the objection raised by McKay (1963) to the Stevens' law: if the perceiving system adjusted with a sort of internal match an infinite number of psychophysical laws could eventually generate a power law.

Furthermore, there is still an important distinction to do: only when the linearity assumption (2.3) holds, $R(I)$ and $\psi(I)$ can, with a slight abuse of notation, be considered both psychophysical laws. In general, the psychophysical law is defined as the relation between the sensation and the stimulus intensity $\psi(I, t)$ and can be obtained through direct psychophysical methods that regard a way of constructing the law by accumulating jnds (Fechner 1860). Instead, within the direct methods introduced by Stevens (Stevens 1956, 1957), the focus is on the pairs (R, I) , hence what is measured are the stimulus intensity and the observed responses of the subjects, that is more a measure of perception than of sensation, and hence independently on their relation to ψ or E . It is indeed well known that different assumptions and scaling hypothesis can lead to different psychophysical laws (Baird and Noma 1978; Gescheider 1997). Identity, equivalence or linearity between R and ψ , and hence between sensation and the lowest or simplest levels of perception, could not be always achieved in the general case. This is another reason for which Lagrangian (3.9) appears to be interesting.

3.9 Summary

A model to describe perception in a steady stimulus case has been structured using variational calculus and analytical mechanics. In particular the psychophysical adaptation phenomenon has been chosen to describe the pattern followed by perception in time. A Lagrangian capable of accounting for both the time-varying features and the classical laws of psychophysics has been built. As a result a free particle Lagrangian, with a time-varying mass, has been obtained and shows several interesting properties: it is a sufficient but not a necessary condition; it allows for different and possible psychophysical laws; it depicts perception as an higher level feature univocally determined by the underpinning neurophysiological processes; it allows to evaluate psychological prothetic continua on an interval scale. Finally, the associated Hamiltonian, that is the energy of the process, follows a decreasing pattern similarly to the response of the firing rate in primary afferent units.

Chapter 4

Perception based on primary afferent units

In this chapter an abstract model of the firing rate in nerve fiber will be developed and used to describe the energy possessed by the neuroelectrical response. A very simplified model of perception will then be built by considering an equivalency between the energy of a nerve fiber and the Hamiltonian of sensation. The resulting psychophysical law and neuroelectrical law are tested on data taken from the literature.

4.1 Model of nerve fiber

The most important model of nerve fiber is the cable-theory, a model whose history is rooted in William Thomson's (Lord Kelvin) work on the signal decay in undersea telegraphic cables, and that has been subsequently applied to neural fibers by Hermann and Cremer. Yet the most important result is its application to describe how action potentials in neurons are initiated and propagated (Hodgkin and Huxley 1952); a fundamental finding followed by several deepening and variations of the model (see for a review Gerstner and Kistler 2002)

Nonetheless, in describing the response of a nerve we will not rely on this important model, since we are not interested in its electrical features. The model suggested in the next sections is instead based on an abstract and coarse-grained description (and interpretation) of the action potentials propagation. Such a model is mainly based on a parallelism between the spiking phenomenon and the De Broglie's wave. Signal propagation inside a nerve can indeed be seen as a wave travelling along the fibers, yet spikes themselves are a discrete phenomenon. Moreover, a similar parallelism is suggested by several empirical findings.

4.1.1 Energy and firing rate

A constant train of impulses generated by a steady stimulus could be schematized as a wave travelling inside the nerve fibers with constant velocity, every spike being a peak of the average whole nerve activity. If such a wave is treated like a De Broglie's wave it carries an energy:

$$E(I, t) = h f(I, t) \quad (4.1)$$

where $f(I, t)$ is the fire rate and h is a constant with the physical dimensions of an action (but of different magnitude from the Planck's constant). This equation, at the level of signal transduction, is coherent with the empirical evidence (found in several animal species) that the amplitude of the receptor potential is linearly related to the frequency of the nerve fiber discharge (Katz 1950; Terzuelo and Washizu 1962; Doving 1964). For a possible physical model of nerve that gives origin to equation (4.1) see Appendix C.

Before choosing a shape for the energy it is very interesting to explore the implications of hypothesis (4.1) on the interpretation of the model.

Inter-spike interval

If hypothesis (4.1) is equated to the Hamiltonian (3.13), since the energy is related to the firing rate then its inverse is both a measure of the wavelength and of the inter-spike interval τ_{ISI} .

$$E = hf \text{ and } E = \frac{\Pi^2}{2m} \rightarrow m = \frac{\Pi^2}{2hf} = \frac{\Pi^2}{2h} \tau_{ISI} = \frac{\Pi^2}{2hv} \lambda \quad (4.2)$$

Thus, once adequately set the dimensions of the variables (see Appendix D) the time-varying mass $m(I, t)$ results to be a measure of the inter-spike interval and increases during psychophysical adaptation, since $\tau_{ISI}(I, t) = 1/f(I, t)$.

Relation between the laws

If hypothesis (4.1) is equated to the Hamiltonian (3.14), the firing rate becomes a measure of the variation in the psychophysical law:

$$E = hf \text{ and } E = \frac{\Pi}{2} \dot{\psi} \rightarrow \dot{\psi} = \frac{2h}{\Pi} f \quad (4.3)$$

Indeed, in the general case, since sensation behaves like an accumulation of energy as in equation (3.16), it appears to be related to the number of summated action potentials, or more in general to the electrical activity of the nerve fiber:

$$\psi(I, t) = c_1 \int h f(I, t) dt + c_2$$

In particular, following equation (3.19), during the psychophysical adaptation phenomenon the sensation at a certain time $t \in \mathcal{T}$ is given by:

$$\psi(I, t) = \psi(I, t_0) - h \int_{t_0}^t f(I, \tau) d\tau$$

hence, the changes in sensation are related to the changes in the total number of action potentials:

$$\psi(I, t) - \psi(I, t_0) = h[N(I, t_0) - N(I, t)]$$

This result could appear strange at a first glance, since usually the firing rate is considered to be proportional to sensation. But there are a couple of considerations that deserve to be done: first, different dependencies on the firing rate could be possible in different sensory systems. For instance, in slowly adapting systems, like many stretch receptors, or cold receptors, nociceptive receptors in the cornea, or pressure receptors of the carotid sinus (Kandel et al. 2000), the firing rate could be taken out of the integral making the magnitude of sensation directly proportional to the firing rate itself (Norwich 1993). Second, but not less important, the previous result holds in the case of a connection between psychophysical adaptation, as the only time features in psychophysical law, and pure adaptation and dynamic range adaptation in a nerve fiber, thus the actual situation is expected to be more complex than this. In particular, the previous equation states that, *during* psychophysical adaptation to a steady stimulus, a finite variation in sensation corresponds to the release of a certain number of action potentials, that is, to a certain value of the firing rate. A situation with time varying stimuli, including also a dynamic part could give totally different results (see chapter six for a discussion).

Constant velocity of the spikes train

Putting together equation (4.2) and equation (4.3) we have that the conservation of momentum (3.12) states that the signal propagates at a constant velocity $v = f\lambda$ inside the fiber:

$$\Pi = m\dot{\psi} = \frac{\Pi^2}{2hv} \lambda \frac{2h}{\Pi} f \rightarrow v = \lambda f$$

hence the signal propagates inside the nerves with the same velocity, independently on its frequency. In particular, different fibers and sensory modalities, having different velocities (Kandel et al. 2000) would have different values of Π .

Action of the nerve fiber

Introducing equation (4.1) into definition (3.5):

$$F[\psi] = h \int_{\mathcal{T}} f(I, t) dt = h[N(I, t_1) - N(I, t_0)]$$

the functional F for a nerve fiber becomes the total action carried by the spikes released during adaptation (or more in greater generality during perception). Hence, the variational requirement (3.4) corresponds to a stationarity constraint on the total electrical activity:

$$\delta F[\psi] = 0 \rightarrow \delta(N(I, t_1) - N(I, t_0)) = 0$$

Changes in perception in this ideal nerve fiber occur trying to achieve stationarity of the total number of generated action potentials (in this particular case minimizing it), and every action potential carries a quantum of action. In our opinion it is a very interesting result that adaptation occurs trying to minimize the number of action potentials generated during the process.

With these results in mind we can now detail a shape for the energy and analyze the resulting equation. To characterize the behavior of the firing rate intensity, the Michaelis-Menten model or Naka-Rushton relation (Naka and Rushton 1966), described in section (1.6), will be chosen and extended to time accounting for pure firing rate adaptation and dynamic range adaptation.

4.2 Naka-Rushton's shape of the energy

In order to characterize the energy we need to shape the firing rate: a widespread behavior in neuroelectrical phenomena is a monotonic increase, as the stimulus intensity raises, until the system reaches a saturation. A behavior that can be recognized in different phases of perception: ranging from the amplitude of several receptor potentials (Lipetz 1969); to the responses of primary afferent units (see for taste: Beidler 1954; hearing: Sachs et al. 1989; touch: Knibestöl 1973, 1975; vision: Naka and Rushton 1966; smell: Duchamp-Viret et al. 1990); higher-level neurons (Lipetz 1969), like those in the rabbit's lateral geniculate nucleus (Cano et al. 2006) or in the cat's and monkey's primary visual cortex (Albrecht and Hamilton 1982; Carandini and Ferster 1997); activation of organized and homogeneous populations of neurons that exhibits similar properties, like columns in the somatosensory and visual cortex, or pools of motor neurons (Gerstner and Kistler 2002). It has also been recently found, by fMRI recordings of a single bilaterally symmetric area in intraparietal and intraoccipital sulci, that the activity peak appears to increase and saturate with the increasing of the amount of information that the visual short-term memory has to retain (Todd and Marois 2004).

Hence, if a Naka-Rushton equation is chosen to model the firing rate and the energy, without accounting for a threshold value, we can write:

$$E(I) = E_m \frac{I^n}{\sigma^n + I^n} \quad (4.4)$$

where E_m is the maximum energy and $\sigma \in \mathbb{R}^n$ is the intensity at which energy attains half of its maximum value. Besides, as it has been detailed in section (1.6), σ can be considered a measure of the dynamic range of the afferent unit: the greater its value the greater the range of intensities in which there's no saturation.

In order to identify energy (4.4) with the Hamiltonian (3.13) we need to introduce the variable time. A possible modeling concerns two fundamental features:

1. *Pure classic adaptation.* The energy decreases in time in order to account to spike frequency adaptation. This can be obtained by reducing the maximum E_m (Wen et al., 2009). The simplest relation is a depletion of the spike frequency with a power law like $E_m(t) = E_m t^{-a}$.

2. *Pure dynamic range adaptation.* The dynamic range of the afferent units has been shown to adapt to different features of the signal (Dean et al., 2005; Wen et al., 2009). A simplified version of this complex behavior can be introduced by taking a value of σ that changes in time to account for dynamic range adaptation. The simplest relation is a power law shift $\sigma^n = Rt^r$.

The combination of this two features leads to a mixed adaptation model (Wen et al., 2009). Energy (4.4) becomes then:

$$E(I, t) = \frac{E_m}{t^a} \frac{I^n}{Rt^r + I^n} \quad (4.5)$$

It is interesting to notice that the previous equation can be brought back, in the limit of negligible decay of the subthreshold level of depolarization, to the firing rate of a neuron with random inter-spike interval distributed like a Gamma function (Stein 1965). Furthermore, a similar firing rate has been used to model the electrically coupled units of a neural network subjected to an external Poisson signal: as a result the system response showed high sensitivity and large dynamic range; besides, the transfer function ranged from a power law to a logarithmic law depending on the relative refractory period of the cells (Copelli et al. 2002). The addition of time features in those models is equivalent to positing a time-varying refractory period and rate of presynaptic excitatory impulses. Moreover, the previous equation can be obtained from Fisher's information entropy using the same assumptions made by Norwich (1993) on the sampling of the stimulus population and the variance of the signal, thus leading to relate the ratio $I^n/(Rt^r)$ to the signal-to-noise ratio (see Appendix D), a feature that sensory systems are well designed to increase (Torre et al. 1995). An alternative derivation of the signal-to-noise ratio, of which equation (4.5) and Norwich's assumptions are just the limit of short-memory process, has also been given for a simple neural networks based on a Brownian motion of the spikes and information theory (Medina 2009).

4.2.1 Threshold correction

Since we are interested in the energy (3.15) involved in perception, we need to account for the value that energy (4.5) attains at the threshold intensity I_0 :

$$E(I_0, t) = E_0 = \frac{E_m}{t^a} \frac{I_0^n}{Rt^r + I_0^n} \quad (4.6)$$

Thus the final energy (and hence the firing rate) becomes:

$$E_P(I, t) = E(I, t) - E(I_0, t) = E_m \frac{Rt^{r-a}(I^n - I_0^n)}{(Rt^r + I^n)(Rt^r + I_0^n)} \quad (4.7)$$

It is straightforward to verify that, for $I_0 \rightarrow 0$, the previous equation turns into energy (4.5). Notice also that equation (4.7) has been obtained with a choice of E_0 that corresponds to an absence of resting activity in the system. Indeed, the term (4.6) is just a correction induced by the existence of an intensity threshold

but does not account for a baseline level of the energy: when the stimulus is at the threshold energy reaches the zero value. This choice can be seen as equivalent to a null spontaneous activity in the nerve (see chapter six for an extension).

Considering now the relation between the exponents a and r , that describe pure spiking frequency adaptation and dynamic range adaptation, two main trends can be identified. In the next sections, for handiness of calculation, will be kept $a = 1$ taking the adaptation scale as the fundamental time scale (see Appendix F).

Pure adaptation faster than dynamic range: $r \leq 1$

If the exponent r , leading the dynamic range adaptation, is lower than or equal to one (or if the exponent a of the pure spike frequency adaptation, is greater than or equal to r) the final adaptation decreases as depicted in figure (4.1).

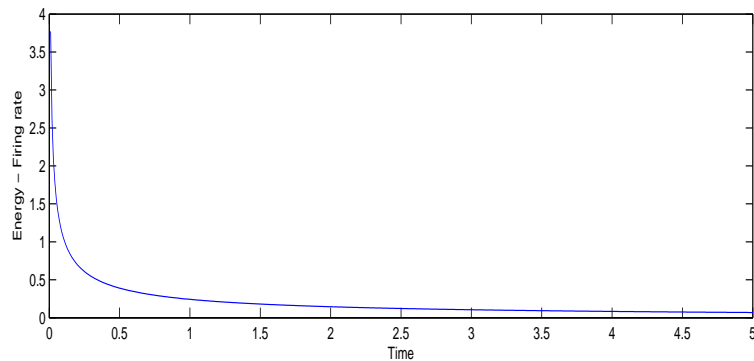


Figure 4.1: Energy/firing rate behavior for $r \leq 1$.

Pure adaptation slower than dynamic range: $r > 1$

If the exponent r is instead greater than one (or if the exponent a is lower than r) the trend of the resulting adaptation behavior is a monotonically increasing one, until it reaches a maximum after which it decreases, as depicted in figure (4.2).

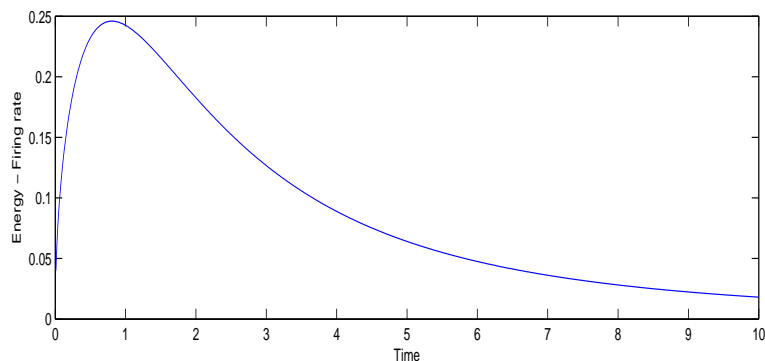


Figure 4.2: Energy/firing rate behavior for $a < r$.

Considering that the system is abruptly impinged by an external stimulus it is very interesting that both the previous trends seems to have a physical meaning. The first one corresponds indeed to an ideal situation in which the nerve fiber tunes immediately to a certain value of the firing rate and then starts to adapt (or similarly, a nerve that starts to adapt from a previously reached value of the firing rate). The second one instead, implies that a fast dynamic range adaptation could still lead the nerve to a gradual increase and tuning in the firing rate in spite of an abrupt stimulation. This would make the nerve a very flexible and reactive structure that could be tuned to a more static or dynamic behavior.

4.3 Perception based on energy (4.7)

Using the energy developed in the previous section we can derive the psychophysical law and explore the plausibility of both the psychophysical and the neuroelectric laws on data taken from literature. To do so we will hypothesize, as in section (2.2.1), that the energy describing the psychophysical behavior, summarized by Lagrangian (3.9) and Hamiltonian (3.13), is related to the energy (4.7) of the nerve fiber.

Identification of energy (4.7) with the Hamiltonian $\mathcal{H}(\psi, \Pi, t)$ can indeed be done by comparison of equations (4.7) and (3.13) with the choice¹:

$$m(I, t) = \frac{(Rt^r + I^n)(Rt^r + I_0^n)}{Rt^{r-1}(I^n - I_0^n)}, \quad E_m = \frac{\Pi^2}{2} \quad (4.8)$$

Hence energy (4.7) can be rewritten as:

$$\mathcal{H}_P(I, t) = \frac{\Pi^2}{2} \frac{Rt^{r-1}(I^n - I_0^n)}{(Rt^r + I^n)(Rt^r + I_0^n)} \quad (4.9)$$

and will now be used to derive the psychophysical law.

4.3.1 Psychophysical law

Integration of equation (3.16) leads to:

$$\psi(I, t) = \frac{2}{\Pi} \int \mathcal{H}_P(I, t) dt$$

where the momentum Π is negative since $\dot{\psi} < 0$ with the only adaptation occurring as time dependent phenomenon. Hence, the psychophysical law related to the shape energy (4.9) becomes, unless of some constant terms (see Appendix F):

$$\psi(I, t) = k \log \left(\frac{Rt^r + I^n}{Rt^r + I_0^n} \right) \quad (4.10)$$

¹Actually, there are other possible choices, but the fundamental difference between them is just a change of the dimensional value of the physical quantities. Choice (4.8) appears to be the most natural from a dimensional point of view. See Appendix E.

with $k \in \mathbb{R}^+$ such that $|\Pi| = kr$.

An interesting result of equation (4.10) is that different limits of its parameters embrace the fundamental power law and logarithmical law. In the limit of an high signal-to-noise ratio, that is when the ratio $I^n/Rt^r \gg 1$, psychophysical law (4.10) behaves like Fechner's law. Taken indeed $\gamma = (Rt^r)^{-1}$ we can write:

$$\psi(I) = k \log \left(\frac{1 + \gamma I^n}{1 + \gamma I_0^n} \right) \tag{4.11}$$

Then, in the limit of $\gamma I^n \rightarrow \infty$, psychophysical law becomes:

$$\psi(I, t) \approx kn \log \left(\frac{I}{I_0} \right)$$

while, in the limit of a low signal-to-noise ratio, that is $I^n/Rt^r \ll 1$ or $\gamma I^n \rightarrow 0$, psychophysical law (4.10) behaves like a correction of the Steven's law as found by Norwich (1993):

$$\psi(I, t) \approx k\gamma(I^n - I_0^n) \tag{4.12}$$

The latter result has been empirically found in the measurement of loudness (Lochner and Burger 1961) and appears to describe the behavior of the psychophysical law near the threshold better than $(I - I_0)^n$ (see also Buus et al. 1998).

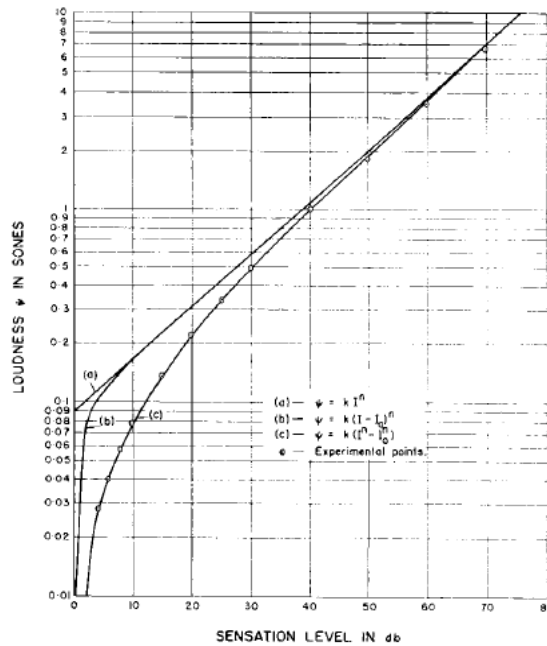


Figure 4.3: Loudness curves given by the relations $\psi = kI^n$, $\psi = k(I - I_0)^n$, and $\psi = k(I^n - I_0^n)$. The experimental points were obtained by Hellman and Zwilowski (Lochner and Burger 1961).

Moreover, in the limit of $I_0 \rightarrow 0$, equation (4.10) becomes:

$$\psi(I, t) = k \log \left(1 + \frac{I^n}{Rt^r} \right) \quad (4.13)$$

The latter expression has the same shape of the psychophysical law firstly proposed by Helmholtz and Delbouf (Murray 1993) with a similar time correction to the law obtained by Norwich (1993) starting from Shannon's entropy. Anyway, it is worthy of notice that it has been derived in a complete different framework. It can also be used to encompass a large spectrum of empirical laws of psychophysics and phenomena (Murray 1993; Norwich 1993, 2010).

Finally, it must be emphasized that equation (4.10) is not *the* psychophysical law; as it has already been stressed several times it is one out of an infinite number of possible laws. In this particular case it is the psychophysical law that for Lagrangian (3.9) is associated with energy (4.7). Moreover, without the choice of the exponent $a = 1$, that selects pure spike frequency adaptation as the fundamental time scale of the system, the solution would have been different (see Appendix F).

4.3.2 Neurelectric law

Since $|\Pi| = kr$ energy (4.9) can now be rewritten as:

$$\mathcal{H}_P(I, t) = \frac{(kr)^2}{2} \frac{Rt^{r-1}(I^n - I_0^n)}{(Rt^r + I^n)(Rt^r + I_0^n)} \quad (4.14)$$

and the frequency of the firing rate becomes:

$$f(I, t) = \frac{(kr)^2}{2h} \frac{Rt^{r-1}(I^n - I_0^n)}{(Rt^r + I^n)(Rt^r + I_0^n)} \quad (4.15)$$

Which seems to have a good agreement with experimental data: examples are given in pictures (4.4) and (4.5).

It is important to notice that, although the Naka-Rushton relation is widely used, the previous equation neither accounts for all the possible psychophysical adaptation trends nor accounts for all the possible neuronal behaviors.

Non-saturating behaviors at the increasing of the stimulus strength have been found for instance in thalamic neurons of the somesthetic system (Mountcastle et al. 1963), in various fast and slow adapting mechano-receptors (Knibestöl 1973, 1975), or in the neurons of the Inferior Colliculus (Dean et al. 2005). Nevertheless, these different rate-level responses could be still accounted in the present framework by relaxing hypothesis (4.1) and considering a value of $h \equiv h(I)$. A similar correction could be considered like a different sensitivity of the system to different stimulus intensities that allows to encompass a wide plethora of neuronal behaviors while keeping a saturating shape of the energy. Moreover, a similar variation wouldn't affect the shape of the psychophysical law (4.10) since does not regard the time dependence of the firing rate.

It is also important to notice that, the value of the firing rate (4.15) appears to be used as a negative feedback to gradually reduce the amount of sensation (4.10),

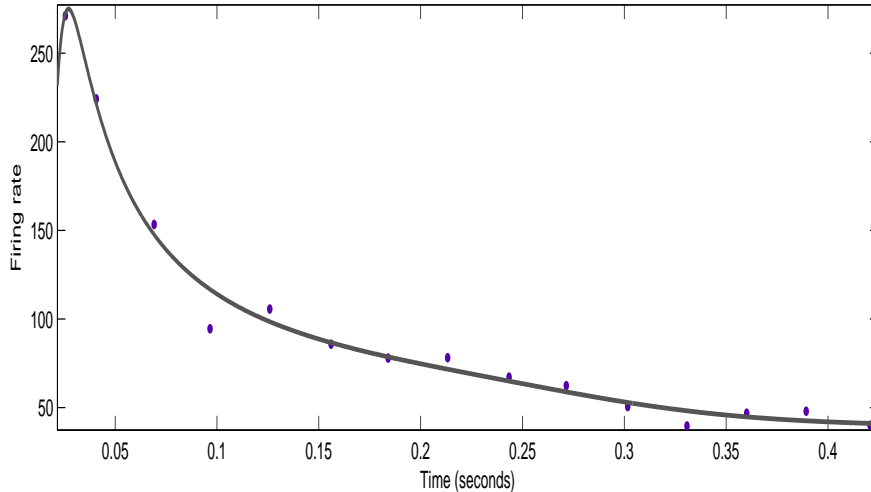


Figure 4.4: Data of Cleland and Enroth-Cugell (1968). Neural adaptation in the on-center ganglion cells of the cat to square-wave inputs of light to the retina. The smooth curve has $R^2 = 0.988$ and $RMSE = 8.7$.

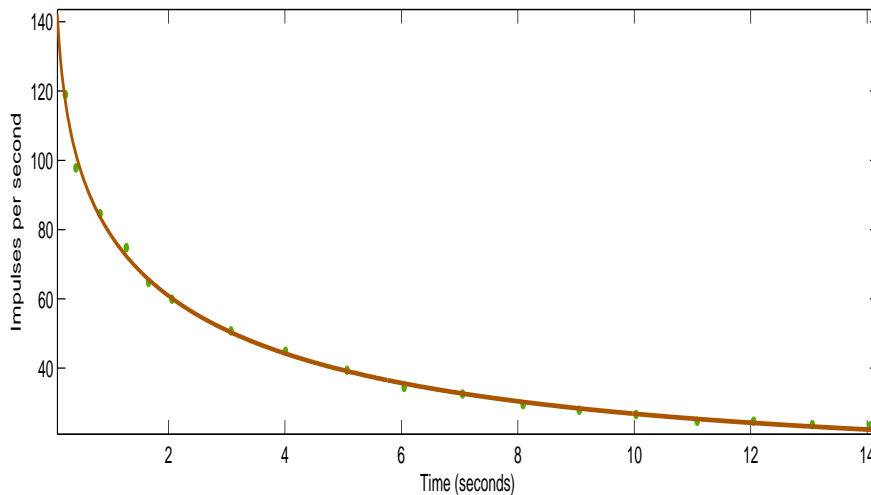


Figure 4.5: Data of Matthews (1931). Neural adaptation of the frog's muscle tendon with two-gram load applied. The smooth curve has $R^2 = 0.99$ and $RMSE = 1.6$.

both the firing rate (4.15) and the psychophysical law (4.10) show a decreasing trend, with the psychophysical law that diminishes more slowly in time. A similar result has been found for instance in the neural response of the chorda tympani to taste stimulation that adapts with a reasonable correspondence between neurophysiological and psychophysiological records (Diamant et al. 1965). Similarly, mechanoreceptors's adaptation precedes the psychophysical one by several seconds (Greenspan and Bolanowski 1996).

Besides, while the firing rate (4.15) shows a saturating trend, psychophysical law (4.10) behaves like a power law or a logarithmic law depending on the value of its parameters. Many sensory modalities exhibits this kind of behavior: single au-

ditory nerve fibers for instance show a saturating behavior in a range dramatically shorter than the effective operating behavioral range of sensation (Viemeister 1988; Wen et al. 2009). The present model, far from pretending to solve a longstanding question like the dynamic range problem, nevertheless stresses the importance of adapting features (Dean et al. 2005; Wen et al. 2009).

Total number of action potentials

As to the total number of action potentials generated in the early t seconds of adaptation, if the system is slow adapting a good approximation can be considered simply the product $f(I, t)t$:

$$\Delta N \approx \frac{(kr)^2}{2h} \frac{\gamma(I^n - I_0^n)}{(1 + \gamma I^n)(1 + \gamma I_0^n)} \quad (4.16)$$

where $\gamma = (Rt^r)^{-1}$.

If the adaptation instead cannot be neglected we need to take the antiderivative of equation (4.15):

$$N(I, t) = \frac{k^2 r}{2h} \log \left(\frac{Rt^r + I_0^n}{Rt^r + I^n} \right) \quad (4.17)$$

Equation (4.17) is a negative monotonic increasing function that approaches zero in the limit of $t \rightarrow \infty$ and can be considered a measure of the number of spikes missing to the total number of action potentials released during the adaptation phenomenon. Indeed, the difference $\Delta N(t, t') \equiv N(I, t') - N(I, t)$, with $t < t'$, is the number of action potentials released during an interval $[t, t']$:

$$\Delta N(t, t') = \frac{k^2 r}{2h} \log \left(\frac{Rt'^r + I_0^n}{Rt'^r + I^n} \frac{Rt^r + I^n}{Rt^r + I_0^n} \right) \quad (4.18)$$

Notice that both equations (4.16) and (4.18) exhibit saturation as the stimulus intensity increases, so that the number of spikes recorded in a given time interval does not differ strongly for high intensity stimuli.

4.4 Preliminary test of the model

In the following subsections some comparisons with data from literature are given for the senses of touch and taste, since, for their nature, they can be considered among the simplest possible modality for which the approximation of a relation between sensation and the response of primary afferent units more likely holds.

4.4.1 Touch

With a broad definition, mechanoreceptive afferent fibers of the glabrous skin of the human hand can be divided into two groups: fast adapting receptors (FA) and slow adapting receptors (SA), where adaptation is referred to their response

to a sustained indentation. In particular, mechanoreceptors's adaptation precedes the psychophysical adaptation by several seconds: the firing rate (4.15) decreases faster then the psychophysical law (4.10) (Greenspan and Bolanowski 1996).

In addition, FA receptors, in spite of their name, do not truly adapt, but show a tonic behavior during a dynamic indentation of the skin: as soon as the stimulus becomes steady, they cease to respond. SA afferents, on the other hand, are sensitive both to a dynamic and to a sustained indentation of the skin. During the latter, in particular, they show a phasic behavior with a low spike frequency adaptation that can last over many seconds or minutes.

Fast adapting receptors

Since FA receptors more then indentation detectors can be considered velocity detectors (Greenspan & Bolanowski, 1996) they can be treated in a steady stimulus framework using the indentation velocity as stimulus intensity and their behavior can be clearly fitted by a log tanh relation (Knibestöl 1973). Fitting of equation (4.16) to the data (red curve in figure 4.6) gives $\gamma \approx 0.03$, a maximum firing rate of about $f_{max} \approx 127.1$ spikes/s and an exponent $n \approx 1.3$, with fit indexes $R^2 = 0.99$ and $RMSE = 3.64$; whereas a power law (blue curve in figure 4.6) like $\psi = kI^n + c$ gives instead $n \approx 0.54$ with $R^2 = 0.95$ and $RMSE = 9.63$, without showing saturation.

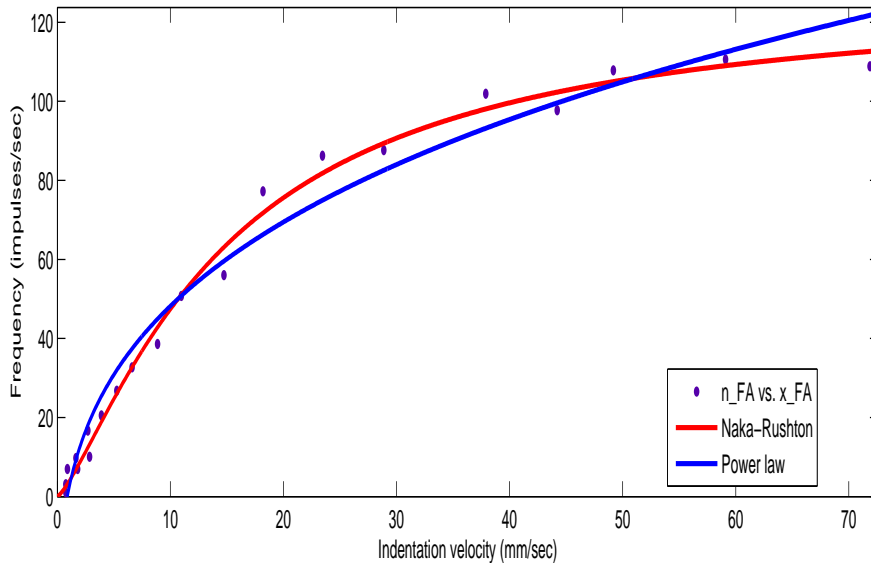


Figure 4.6: Data from Knibestöl (1973), fig. 9A. Stimulus-response function of a fast adapting (FA) receptor to the velocity of indentation.

Slow adapting receptors

A similar result holds for SA mechanoreceptors. Their trend can be divided into a dynamic part, due to dynamic indentation of the skin, and a static part, due to the sustained indentation. Knibestöl (1975) specified then two possible measures

of firing rate: the total sum of action potential generated in one second (TS) including both the dynamic and the static parts; and the mean firing rate of the last 0.5 seconds of static indentation (MF).

As to the measure TS, since firing rate adaptation is negligible, the total number of spikes can be measured by equation (4.16): a fit to data of Knibestöl (1975) and Knibestöl and Vallbo (1980) (see pictures 4.8 and 4.7) gives a threshold of about $I_0 \approx 0.50$ mm, close to the experimental mean value 0.51 ± 0.06 mm, maximum firing rates f_{max} of 28.5 and 53.1 spikes/s, γ parameters of about 0.6 and 0.8, and exponent n values of 4.0 and 6.1, with fit indexes $R^2 = 0.99$ and $RMSE$ of 1.0 and 1.5. The high value of n is due to the sigmoidal shape induced by the dynamic part of the stimulation. Equation (4.16) appears to be a good description of the total number of action potentials, including the dynamic part, when the system has a slow adaptation rate.

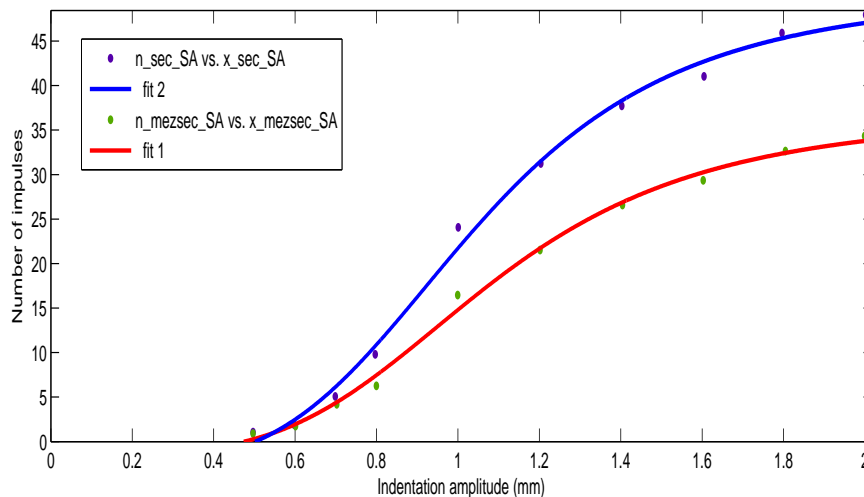


Figure 4.7: Data from Knibestöl and Vallbo (1980), fig. 3. Stimulus-response plots of a SA-I receptor stimulated with indentation of 0.5 (red line) and 1.0 (blue line) secs of duration.

As to the measure MF, the fit gives, for both equations (4.16) and (4.18), a value of the threshold $I_0 \approx 0.85$ mm, close to the experimental mean value 0.89 ± 0.09 mm, and an exponent $n \approx 1.97$, with fit indexes: $R^2 = 0.99$, $RMSE = 0.7$ (see red curve in picture 4.8). The variability of the parameter γ , that ranges from 255 in equation (4.16) to 718 in equation (4.18), appears to be related to a difficulty in computing the correct slope from data that do not show a saturation: indeed both the equations fail in predicting the maximum firing rate.

Relation between psychophysical and neural responses

Finally, a comparison of subjective and neural responses has been given in Knibestöl and Vallbo (1980) emphasizing an absence of correlation between psychophysical and neural exponents. Indeed, the average trend of the psychophysical responses is linear (albeit inter-individual differences reveal both accelerating and decelerating

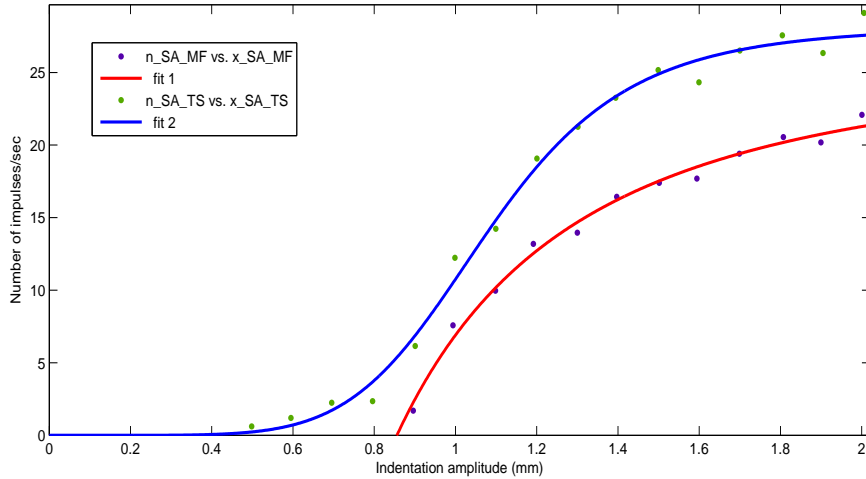


Figure 4.8: Data from Knibestöl (1975), fig. 5. Stimulus-response plot for a SA-I receptor. TS-plot (green points) and MF-plot (blue points).

trends) while the neural average function is clearly decelerating. Mean exponents, obtained with a power law in the same group of subjects, attains a value of 1.18 for the psychophysical law and 0.72 for the neuroelectric response.

Considering now, as a case of study, a subject with a clear difference between psychophysical and neural exponents the fit of equations (4.11) and (4.16) leads to interesting results. Knibestöl and Vallbo (1980) indeed stimulated the subject's hand in three different locations as in figure (4.9).

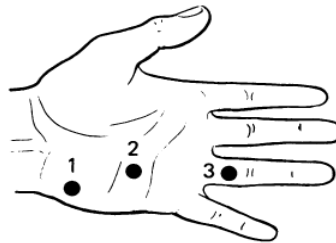


Figure 4.9: Different locations of stimulation.

Data recorded on location number three (see pictures 4.10) exhibits a clearly divergent trend between the psychophysical and the neural exponents (1.24 against 0.40 obtained with power law). Psychophysical law (4.10) gives $\gamma \approx 0.2$ and $n \approx 1.3$, with $R^2 = 0.97$, and $RMSE = 1.6$; while the fit of neural data gives $\gamma \approx 3.2$, $f_{max} \approx 87.8$ spikes/s, and $n \approx 1.15$, with $R^2 = 0.98$ and $RMSE = 2.4$. The agreement between the two set of parameters can be considered quite good. In particular, the psychophysical and the neural exponents appear now to be compatible. This result is particularly interesting since it suggests that using different laws there still could be the exponents identity suggested by several authors (Stevens 1970; Barlow 1972; Norwich 1993).

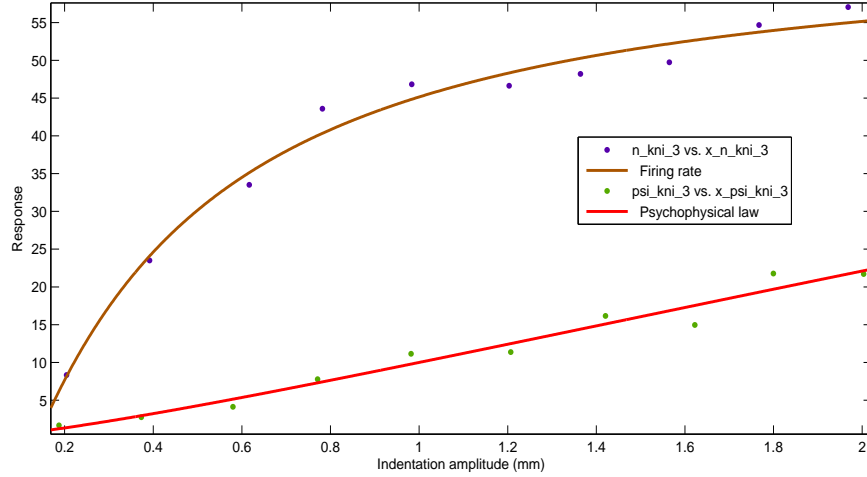


Figure 4.10: Data from Knibestöl and Vallbo (1980), fig. 9, plot 3. Psychophysical and neural responses at location number three to skin indentation stimuli.

At the location number one, instead, that show a slightly increased difference between the psychophysical and the neural exponents (1.33 against 0.38 obtained with power law), the psychophysical law gives $\gamma \approx 0.98$, $n \approx 2.05$ with $R^2 = 0.98$ and $RMSE = 0.98$; while the fit of the neural data gives $\gamma \approx 62.05$, $n \approx 0.53$, with $R^2 = 0.99$ and $RMSE = 1.65$, but fails to achieve a maximum firing rate since the neural data show an increasing trend for high depths of indentation. Nevertheless, forcing equation (4.16) to take the psychophysical value of the exponent still leads to an acceptable fit of the data with $I_0 \approx 0.12$ mm, $\gamma \approx 6.4$ and a maximum firing rate $f_{max} \approx 51.5$ spikes/s, with $R^2 = 0.98$, $RMSE = 1.97$.

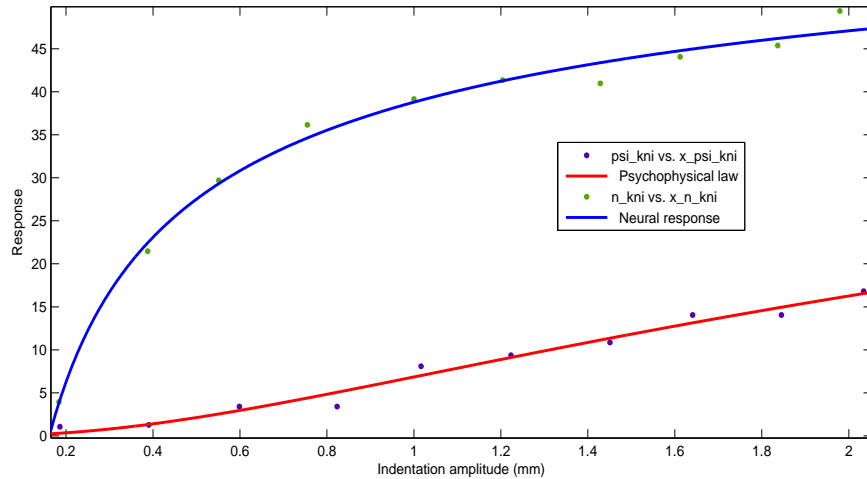


Figure 4.11: Data from Knibestöl and Vallbo (1980), fig. 9, plot 1. Psychophysical and neural responses at location number one to skin indentation stimuli.

In addition, as it has been suggested in section (4.3.2), a term like $h \equiv h(I)$

could allow the firing rate to depend on individual variations of the nerve while attaining different patterns and without affecting neither the Naka-Rushton shape of the energy nor the psychophysical law. The system could be for instance less sensitive to stimuli near the threshold, having thus a dependance like $h \approx I^{-\delta}$. The addition of such a term to equation (4.15), with a fixed threshold of $I_0 = 0.16$ mm, gives a maximum firing rate $f_{max} \approx 65.7$ spikes/s, and values of the parameters $\gamma \approx 32.6$, $n \approx 2.18$ and $\delta \approx 0.23$, with indexes of fit $R^2 = 0.99$, and $RMSE = 1.6$. The value of $d < 1$ implies that, for this subject, the firing rate increases slowly at high intensities instead of saturating (f_{max} can still be considered the maximum firing rate with a slight abuse of notation) and this is what seems to happen in the data as can be seen in picture (4.11). Moreover, the value of the psychophysical exponent is now very close to the one given by the psychophysical law: $n \approx 2$.

A similar result can be achieved with location number two, that show the greatest difference between psychophysical and neural exponents (1.60 against 0.38 obtained with power law). The psychophysical law gives $\gamma \approx 1.3$ and $n \approx 3.0$, with fit indexes $R^2 = 0.99$, and $RMSE = 0.6$; while the fit of neural data (it must be noticed that the data were few compared to the other subjects) gives $n \approx 0.22$ with $R^2 = 9.96$, $RMSE = 4.3$. Forcing anyway the exponent of the power law, and introducing a correction to h , lead to a fit with $R^2 = 0.97$, $RMSE = 3.39$.

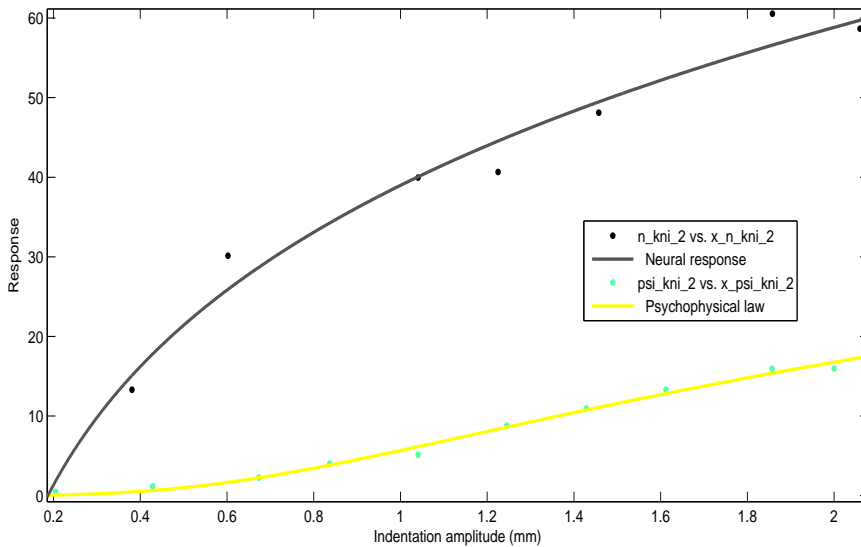


Figure 4.12: Data from Knibestöl and Vallbo (1980), fig. 9, plot 2. Psychophysical and neural responses at location number two to skin indentation stimuli.

As a final notice: the value of the threshold I_0 obtained by the psychophysical law is often close to zero, while in for neural data ranges between $0.14 - 0.18$ mm; forcing however the psychophysical and the neural laws to have the same threshold value does not introduce significant variations in the others parameters.

These results emphasize on one side how much those parameters are sensitive to slight changes in the model: broad confidence intervals make indeed very likely to find a common set of parameters. Moreover, an adequate number of parameters

can always end in an overfit of the data, being the rationale behind a contrived improvement of the fitness quality. On the other hand, considering the previous results as preliminary, they emphasize that psychophysical law and neural law could be related through some abstract and general principle.

4.4.2 Taste

The response of the chorda tympani nerve to salt stimulation almost completely adapts with a reasonable correspondence between neurophysiological and psychophysiological records (Diamant et al. 1965). In particular, the summated electrical response shows 95% of adaptation in about 50 seconds, while psychophysical adaptation ranges between 79 and 122 seconds. Equation (4.15) decreases faster than psychophysical law (4.10). Moreover, peaks of activity in the response to sucrose stimulation correlates with subjective responses (Diamant et al. 1965). More in general, a correlation between subjective estimation and summated electrical activity has been found for different concentrations of salt, sucrose and citric acid (Borg et al. 1967).

Since the maximum height of the electrical activity is defined as a record of the whole spikes elicited by the stimulation (Lipetz 1969), a comparison should be done between psychophysical law (4.10) and the total number of summated action potential accumulated during the rising phase. However, since equation (3.19) depicts adaptation like a process of decreasing energy until extinction, the total electrical activity generated during adaptation should be at least proportional to the total activity generated during excitation.

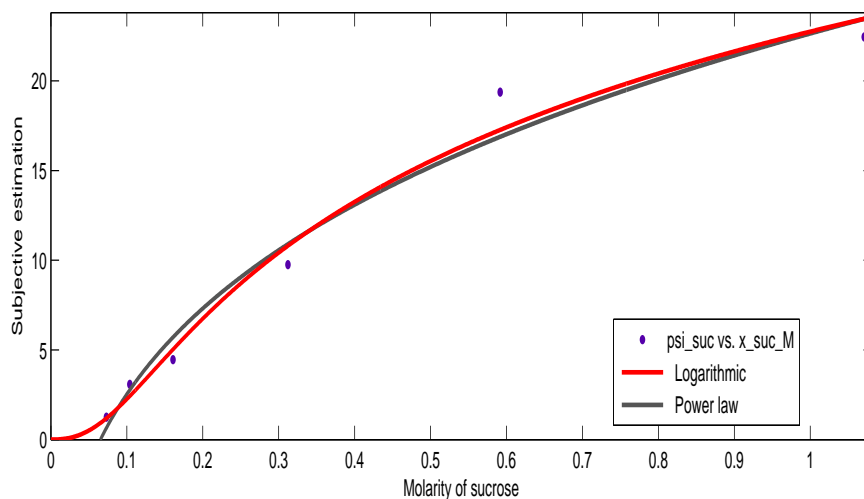


Figure 4.13: Data from Borg et al. (1967), fig. 6. Subject's estimation plotted against the molarity of sucrose solution.

Equation (4.11), fitted to sucrose data (red curve in fig. 4.13), gives a value of the threshold $I_0 \approx 10^{-9}M$, a value of the parameter $\gamma \approx 204$, and an exponent $n \approx 2.47$, with indexes of fit $R^2 = 0.9$ and $RMSE = 1.9$; whereas a power law (gray curve in fig. 4.13) of the kind $\psi = kI^n + c$ gives $n \approx 0.27$ with $R^2 = 0.9$ and

$RMSE = 1.9$. Setting a naught value of the threshold, $I_0 = 0$, in equation (4.11) allows to further improve the fit ($R^2 = 0.99, RMSE = 0.5$) but does not change the value of the exponent n . The results can be seen in figure (4.13).

The equation for fitting the summated electrical activity could be derived from equation (4.18) in the limit of both $I_0, t \rightarrow 0$ and $t' \rightarrow \infty$ giving:

$$N_{Peak} \approx A \log \left(\frac{I}{I_0} \right)^n + C_\infty \quad (4.19)$$

with $A, C_\infty \in \mathbb{R}^+$. The latter in particular is a divergent term at exactly $t = 0$ only because the combination of three limits leads the model into a situation out of the bulk condition in which energy (4.14) has been built.

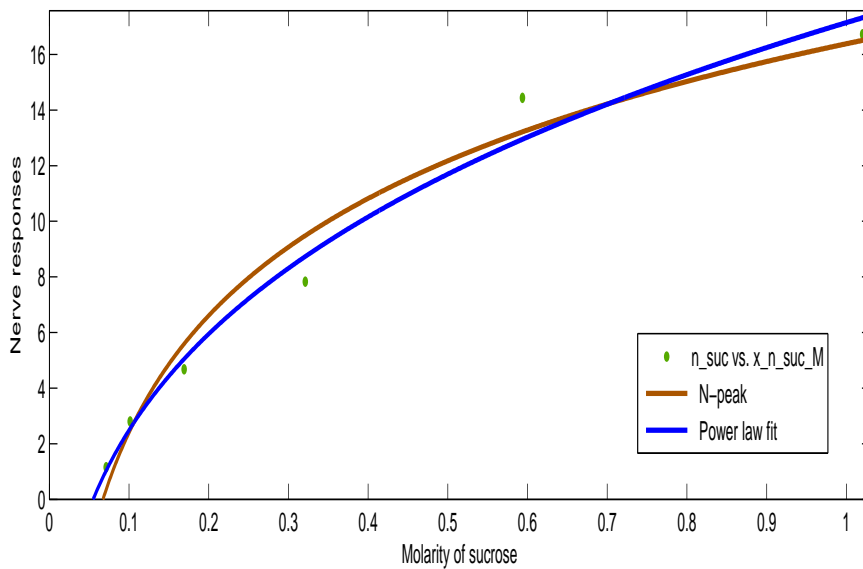


Figure 4.14: Data from Borg et al. (1967), fig. 6. Nerve responses plotted against the molarity of sucrose solution.

In spite of this, equation (4.19), fitted to neural data (brown curve in 4.14), gives a value of the exponent $n \approx 2.32$ with fit indexes $R^2 = 0.97, RMSE = 1.7$; whereas a power law like $\psi = kI^n + c$ (blue curve in 4.14) gives $n \approx 0.28$ with $R^2 = 0.98, RMSE = 1.1$). In spite of the broad confidence bounds for both logarithmic and power laws, the agreement can be considered quite good: in both cases indeed the exponents exhibit the same value. In addition, the higher the signal-to-noise ratio, the more equation (4.19) resembles the psychophysical law (4.10). This seems to agree with the observation that psychophysical and neurophysiological responses are both correctly described by a logarithmic law with similar parameters (Borg et al., 1967). Furthermore, the neural and the psychophysical exponents are very close one to each other like in the power law case.

Nevertheless, it must be stressed that equation (4.19) has been obtained with an assumption of proportionality between the activity generated during adaptation and the activity generated during the rising phase of perception. Moreover, the

combination of the three limits makes the energy more sensitive to fluctuations in the data. As an example, when equation (4.11) is fitted to the acid citric data, that show higher variability than the sucrose data, it gives a good result for the psychophysical law: $\gamma \approx 6213$, $n \approx 1.54$ with $R^2 = 0.99$ and $RMSE = 0.5$ (against a power law $n \approx 0.50$ and $R^2 = 0.97$ an $RMSE = 1.89$); while the fitting of the neural data reveals to be weak, giving $n \approx 2.26$ with $R^2 = 0.88$ and $RMSE = 5.03$ (against the result of a power law $n \approx 0.69$ with $R^2 = 0.99$, $RMSE = 1.087$).

4.5 Summary

In this chapter an abstract description of the firing rate has been given in terms of a De Broglie's wave. Hence the energy carried by the spikes train is linearly related to its frequency. Under this assumption, an interpretation of the formalism that links the psychophysical response to the neurophysiological background of primary afferent units has been given. In detail, the modulating function $m(I, t)$ that characterizes Lagrangian (3.9) appears to be a measure of the inter-spike interval, and hence is related to the wavelength of the De Broglie wave; the spike frequency appears to be a measure of the changes in time of sensation, while the conservation of the conjugate momentum implies that the signal travels with a constant velocity inside the nerve, independently on the magnitude of the spike frequency.

In addition, the variational requirement underpinning the whole behavior of the system appears to be the minimization of the total number of action potentials released during the adaptation phenomenon.

A structure of the energy describing the neuroelectric behavior has then been modeled on the Naka-Rushton relation and extended to time by the addition of pure spike frequency adaptation and dynamic range adaptation. The resulting energy has been used to obtain the psychophysical law by means of the Euler-Lagrange equation. As a result, sensation appears to be described by an equation capable of switching from a power law to a logarithmic law depending on the signal-to-noise ratio. Moreover, a very similar law had been already proposed by Delbouf and Helmholtz (Murray 1993) and subsequently obtained by Norwich (1993) moving from Shannon's information entropy.

Finally, these preliminary results of the model have been tested on data on the senses of taste and touch. The agreement is particularly good with the latter for which the approximation of a straight connection between sensation and the response of primary afferent units holds better than in the other senses. In particular, the psychophysical law and the neuroelectrical law of the model appear to have the same exponents as posited by many authors (Stevens 1970; Barlow 1972).

Chapter 5

Laws of psychophysics

In this chapter will be derived some laws of classical psychophysics and some empirical laws that describe the behavior of the senses. The treatise will be mainly based on the framework developed before except for only one assumption of discreteness that will rely on mechanical statistical considerations.

5.1 Statistical Mechanics and Perception

Statistical mechanics is introduced in this thesis with a twofold purpose: on one hand it allows to discretize the senses by focusing on their quantized nature at their basic level; on the other hand it is useful to introduce a fundamental feature of sensory systems that the framework outlined in the previous sections cannot account for, that is the limited resolving power of the psychophysical systems.

As it has already been pointed out in section (2.1), in spite of its discrete nature the world appears to our perception as continuous. Nevertheless, on a physical and chemical perspective our senses are able to grasp its discreteness: chemoreceptors detect molecules and atoms; vision receptors detect single quanta of light; the sense of hearing, although it is not quantized, still at the eardrum level is capable of appreciating an atom's width variation in pressure (Torre et al. 1995; Gescheider 1997). Yet our perception of the world is smooth, continuous and coarse-grained, as if somewhere in between receptors transduction and perception there were a transition to continuousness. In other words, Weber's fraction can not appreciate an infinitesimally small difference in the intensity of the stimulus.

In order to simplify the problem we will keep to consider a steady stimulus situation, so that the time dependence of the model is due only to adaptation and the Hamiltonian is a family of patterns in time labeled by the parameter $I \in \mathbb{R}^+$.

5.1.1 Energy jnds

Bijjective and continuous relations between energy and stimulus intensity, like equations (3.13) or (4.4), cannot account for the limited resolving power of sensory modalities, since in those relations for any value of the stimulus intensity there is a corresponding value of the energy. Nevertheless, from a statistical mechanical perspective, different states of a system, corresponding to different points in the state

space \mathcal{S} or in the phase space Γ , should be considered equivalent by the perceiving system if they belong to the set of the states whose internal energy lies in between certain values of the Hamiltonian H and $H + \Delta H$. In particular, in hypothesis (2.9), we have posited a relation between the energy and the neuroelectric behavior. Hence the idea of enclosing perception in a statistical mechanical framework leads to consider the perceiving system as incapable of distinguish the difference between neuroelectric responses of intensities E and $E + \Delta E$.

Thus, different stimulus situations of intensity I and $I + \Delta I$, corresponding to different states in \mathcal{S} or in Γ , could be perceived as equal if they belonged to the set of the states whose internal energy lies between E and $E + \Delta E$. This seems also to agree with the observation that there can be peripheral activity without a corresponding behavioral correlate McKenna (1985).

As a matter of fact, a minimum ΔE behaves as an energy-jnd that restrains all the other quantities. The limited resolving power of the system will be then introduced with the strong ¹ approximation of holding this jnd constant:

$$\Delta E(I) \equiv \epsilon \quad (5.1)$$

independently on a possible dependence of the resolving power by the magnitude of the stimulus itself. Hence, ϵ is the smallest physiological difference between two levels of the internal energy elicited by a particular sensory stimulus. This hypothesis from a certain point of view parallels Fechner's hypothesis of the constant jnd but shifts it on an internal energy context in which, as equation (3.16) suggests, perception can be regarded as a cumulative process. A value of the energy $E(I, t)$ can then be obtained by accumulating $N(I, t)$ energy-jnds:

$$E(I, t) = \epsilon N(I, t) \quad (5.2)$$

Equating with expression (4.5):

$$N(I, t) = \frac{E}{\epsilon} = \frac{E_m}{\epsilon t^a} \frac{I^n}{Rt^r + I^n} \quad (5.3)$$

or with the threshold correction of (4.14):

$$N_P(I, t) = \frac{E_P(I, t)}{\epsilon} = \frac{(kr)^2}{2\epsilon} \frac{Rt^{r-a}(I^n - I_0^n)}{(Rt^r + I^n)(Rt^r + I_0^n)} \quad (5.4)$$

The saturation of energy implies then a maximum in the number of energy-jnds that can be accumulated by a sensory modality. In particular, considering a constant time situation, so that $\gamma = (Rt^r)^{-1}$, we can write:

$$N_P(I) = N_0 \frac{\gamma(I^n - I_0^n)}{(1 + \gamma I^n)(1 + \gamma I_0^n)} \quad (5.5)$$

¹In general the relation could be a more complex one, like $E = \int \epsilon(I)\rho(I)dI$, the idea of keeping the same value for all the energy-jnds is a rather strong assumption, yet is the simplest to do as a starting point.

once set:

$$N_0 \equiv \frac{(kr)^2}{2\epsilon t^a} \quad (5.6)$$

that is the maximum number of energy-jnds if the threshold I_0 is equal to zero. Indeed, once taken the limit $I \rightarrow \infty$:

$$\lim_{I \rightarrow \infty} N_P(I) = \frac{N_0}{1 + \gamma I_0^n} \equiv N_\infty \quad (5.7)$$

is the maximum number of energy-jnds in presence of a threshold I_0 .

Notice also that equation (5.2) is strictly connected with hypothesis (4.1). In particular, in a highly discretized system each jnd would be a spike. N would then be the number of spikes generated in one second by the firing rate f . Each spike carrying a quantum of action h and energy ϵ .

A final notice deserve to be done. In a mechanical statistical treatise the number of the state that are equivalent on an energetical base is measured by the entropy. See Appendix G for the behavior of entropy for these systems and its relation with simple reaction times: Pieron's law can indeed be derived moving from the entropy of the system and considering the time that is needed to the perceiving system to span the space of the equivalent states.

5.1.2 The Bloch-Charpentier law

One of the most important empirical law of sensation was defined in two separated papers by Bloch (1885) and Charpentier (1885) by applying to vision the Bunsen-Roscoe law. In particular, it states that the minimum perceptible light intensity I_{Th} is a function of the duration t of the stimulus:

$$I_{Th}t = C \quad (5.8)$$

where C is a constant with the dimension of a physical energy. In particular there is a minimum value I_∞ of the threshold below which no light stimulus is perceptible:

$$I_{Th} \geq I_\infty \quad (5.9)$$

In addition, the Bloch law holds only for small values of time, namely $t < 0.1 - 0.3$ seconds, after which a most general relation discovered by Blondel and Rey (1912) is needed:

$$\frac{I_{Th}}{I_\infty} = 1 + \frac{a}{t} \quad (5.10)$$

where a is known as the Blondel-Rey constant.

Another generalization was given by Garner (1947):

$$I_{Th}t^\delta = C \quad (5.11)$$

and can be mixed with the Blondel-Rey generalization to give:

$$\frac{I_{Th}}{I_\infty} = 1 + \frac{a}{t^\delta} \quad (5.12)$$

It is also worthy of notice, that the same law seems to hold for the sense of hearing (Norwich 1993; Coren et al. 1999) and is commonly used for temporal summation (Bunsen-Roscoe law) or spatial summation (Ricco's law) in neurons. Moreover, it resembles another fundamental relation in biomedical application: the Weiss-Lapicque law.

Lapicque's law

By changing the Weiss' law Lapicque (1907, 1909) stated that the current I required to excite a variety of irritable tissues can be written as a function of the duration d of the impulse impinging the tissue:

$$I = \frac{k}{d} + b \quad (5.13)$$

where b is then the current needed to stimulating with a pulse of finite duration and is called the rheobase. The previous equation can be rewritten as:

$$\frac{I}{b} = 1 + \frac{c}{d} \quad (5.14)$$

where c is the chronaxie (that is the value at which the current is twice the rheobase). The former relation is tissue specific and is very similar to the Blondel-Rey law (5.10). Furthermore, a generalization of Lapicque's law has been given by Ayers et al. (1986) and is:

$$\frac{I}{b} = 1 + \frac{c}{d^\alpha} \quad (5.15)$$

that is exactly equation (5.12).

Derivation in the model

Considering now equation (4.7), we can derive the previous equations with a certain degree of approximation. Taking indeed the limit $t \rightarrow 0$ energy (4.7) can be rewritten as:

$$\lim_{t \rightarrow 0} E_P \approx \frac{Rt^{r-a}(kr)^2}{2} \frac{I^n - I_0^n}{I^n I_0^n}$$

that can be rewritten as:

$$E_P \approx \frac{Rt^{r-a}(kr)^2 I^n - I_0^n I_0^n}{2} \frac{I_0^n}{I_0^{2n} I^n}$$

If we consider now the intensity threshold I_0 as the minimum possible detectable threshold, since the stimulus intensity I is expected to be always greater or equal to I_0 , we can approximate with a slight abuse of notation:

$$E_P \leq \frac{Rt^{r-1}(kr)^2 I^n - I_0^n}{2} \frac{I_0^n}{I_0^{2n}}$$

that can be rearranged in:

$$I^n \geq I_0^n + \frac{2EI_0^{2n}}{(kr)^2 Rt^{r-a}}$$

Now, a discretization of the energy like (5.1) implies that the energy E_p must be at least equal to the value ϵ . Hence, if we consider the threshold intensity I_{th} as the one for which the value of the energy attains the value ϵ we have:

$$I_{Th}^n \geq I_0^n + \frac{2\epsilon I_0^{2n}}{(kr)^2 Rt^{r-a}} \quad (5.16)$$

Furthermore, since the energy-jnd is expected to be very small, a Taylor expansion for the previous equation leads to:

$$\frac{I_{Th}}{I_0} \geq 1 + \frac{2\epsilon I_0^n}{n(kr)^2 Rt^{r-a}}$$

that once set $a = (2\epsilon I_0^n)/(n(kr)^2 R)$ and $\delta = r - a$ gives:

$$\frac{I_{Th}}{I_0} \geq 1 + \frac{a}{t^\delta} \quad (5.17)$$

Expression (5.17) is a further generalization of the Bloch-Charpentier law and of the Lopicque law, similar to the one made by Blondel and Rey (1912). Notice that in particular is always true that:

$$I_{Th} \geq I_0$$

that is equation (5.9). So the actual threshold is always greater or equal than a particular minimum required value².

Moreover, if t is very close to zero, equation (5.16) can be rewritten as:

²It is interesting to notice that I_0 was defined as the threshold value at which the energy of perception \mathcal{H}_P is equal to zero. Hence it appears sensible that the actual threshold I_{th} appears to be greater or equal than that minimum value.

$$I_{Th}^n \geq \frac{2\epsilon I_0^{2n}}{(kr)^2 R t^{r-a}}$$

and then:

$$I_{Th}^n t^{r-a} \geq \frac{2\epsilon I_0^{2n}}{(kr)^2 R}$$

that can be rewritten as:

$$I_{Th} t^\delta \geq C \quad \text{where} \quad \delta = \frac{r-a}{n}, \quad C = \left(\frac{2\epsilon I_0^{2n}}{(kr)^2 R} \right)^{\frac{1}{n}}$$

that is like the generalization (5.11) of the Bloch-Charpentier law proposed by Garner (1947). As a final notice, it is interesting that to have the Bloch law for vision we need $n = 1$. In the case of light then, to have also $\delta = 1$, we need $r - a = 1$. Thus the dynamic range adaptation in the pathways of vision is expected to be faster than the spike frequency adaptation. Furthermore, since in general $0 < \delta \leq 1$, we could expect that $r \leq n + a$ for a given sensory modality.

5.1.3 The classical jnds

Using equation (4.11) the value of the classical jnd $\Delta\psi$ can be derived. Taking indeed the value of the jnd as:

$$\Delta\psi = \psi(I + \Delta I) - \psi(I) \tag{5.18}$$

we have:

$$\Delta\psi = k \log \left(\frac{1 + \gamma(I + \Delta I)^n}{1 + \gamma I^n} \right)$$

that can be rewritten as:

$$\Delta\psi = k \log \left(\frac{1 + \gamma w(I) I^n}{1 + \gamma I^n} \right) \tag{5.19}$$

where:

$$w(I) \equiv \left(1 + \frac{\Delta I}{I} \right)^n \tag{5.20}$$

is a function directly related to the Weber fraction $\Delta I/I$. However, since we are interested in verify if the model can enclose classical psychophysics, we can hold (5.20) constant, thus $w(I) \equiv w$. Hence, taking the limit $I \rightarrow \infty$, in which psychophysical law (4.13) behaves like a Fechner's law, and expanding (5.19) in Taylor series arrested at the first order:

$$\lim_{I \rightarrow \infty} \Delta\psi \approx k \log \left(\frac{w\gamma I^n}{\gamma I^n} \right) = k \log w$$

that is exactly the constant Fechner's jnd $\Delta\psi = c$, with $c = k \log w \in \mathbb{R}^+$.
Taking instead the ratio:

$$\frac{\Delta\psi}{\psi} = k \left[\frac{\log(1 + \gamma w(I)I^n)}{\log(1 + \gamma I^n)} - 1 \right]$$

and the limit $I \rightarrow 0$, in which psychophysical law (4.13) behaves like a Stevens's law, and expanding in Taylor series arrested at the first order:

$$\lim_{I \rightarrow 0} \frac{\Delta\psi}{\psi} \approx k \left[\frac{c\gamma I^n}{\gamma I^n} - 1 \right] = k[w - 1]$$

that is the Ekman's law (Ekman 1959) $\Delta\psi = c\psi$ with $c = k[w - 1] \in \mathbb{R}^+$.

Equation (5.19) can then be considered a generalization of the jnd $\Delta\psi$ and can be easily calculated once known the value of the Weber fraction.

5.1.4 The Weber fraction

Rewriting energy (4.14) as:

$$E = \frac{(kr)^2}{2t^a} \left[\frac{\gamma I^n}{1 + \gamma I^n} - \frac{\gamma I_0^n}{1 + \gamma I_0^n} \right] \quad (5.21)$$

with $\gamma = (Rt^r)^{-1}$, the Weber fraction $\Delta I/I$ can be derived by considering the difference between the energies $E + \Delta E$ and E .

Taking indeed:

$$\Delta E = \frac{(kr)^2}{2t^a} \left[\frac{\gamma I^n (1 + \frac{\Delta I}{I})^n}{1 + \gamma I^n (1 + \frac{\Delta I}{I})^n} - \frac{\gamma I^n}{1 + \gamma I^n} \right]$$

we can see that the presence of a threshold I_0 does not affect the result. Using now definition (5.20) we can write:

$$\Delta E = \frac{(kr)^2}{2t^a} \left[\frac{\gamma I^n w^n}{1 + \gamma I^n w^n} - \frac{\gamma I^n}{1 + \gamma I^n} \right]$$

where, making use of the hypothesis (5.1), and thus considering the slightest difference in energy ΔE that leads to a difference in perception, we have:

$$\epsilon = \frac{(kr)^2}{2t^a} \left[\frac{\gamma I^n w^n}{1 + \gamma I^n w^n} - \frac{\gamma I^n}{1 + \gamma I^n} \right]$$

that using definition (5.7) and expressing w as a function of any other quantity:

$$w(I) = \left(\frac{\frac{1}{\gamma} + (N_0 + 1)I^n}{N_0 - (1 + \gamma I^n)} \right) \frac{1}{I^n}$$

and finally by the definition of w :

$$\frac{\Delta I}{I} = \left(\frac{\frac{1}{\gamma} + (N_0 + 1)I^n}{N_0 - (1 + \gamma I^n)} \right)^{\frac{1}{n}} \frac{1}{I} - 1 \quad (5.22)$$

Equation (5.22), in spite of being still a rough approximation of the actual Weber's fraction exhibits several interesting features:

1. In the limit $I \rightarrow 0$, the Weber fraction (5.22) follow a typical hyperbolic trend:

$$\frac{\Delta I}{I} \approx \left(\frac{1}{\gamma(N_0 - 1)} \right)^{\frac{1}{n}} \frac{1}{I}$$

2. The function decreases until it reaches a minimum at the value:

$$I_{min} = \left(\frac{1}{\gamma} \frac{N_0 - 1}{N_0 + 1} \right)^{1/n}$$

at which attains the positive value:

$$\frac{\Delta I}{I} = \left(\frac{N_0 + 1}{N_0 - 1} \right)^{2/n} - 1 = k_W \quad (5.23)$$

Hence, in a neighborhood of this minimum, equation (5.22) can be approximated by the constant Weber's ratio k_W . The extension of this neighborhood can be roughly estimated as the range in which (5.22) is far from its extremes:

$$\left(\frac{1}{\gamma(N_0 + 1)} \right)^{1/n} \ll I \ll \left(\frac{N_0 - 1}{\gamma} \right)^{1/n}$$

corresponding to an intensity span of the order:

$$I_{max}/I_{min} \approx N_0^{2/n}$$

The higher the Stevens' exponent n , the shorter the plateau. This result agrees with the experimental finding that the greater the range of sensation, the lower is the Stevens' exponent (Teghtsoonian 1971). In particular, the higher the value N_0 , the larger the plateau, that is the higher the maximum

firing rate achievable by a sensory modality the higher the extension of the region in which the Weber fraction can be considered constant.

3. When the stimulus intensity I reaches a value R such that $N_0 = 1 + \gamma R^n$, the denominator of the function $w(I)$ becomes singular and the Weber fraction diverges. A terminal rising portion has been found for several sensory modalities like in the sense of taste and vision, or with different stimulations like pressure on a single Meissner's corpuscle, heaviness, flavor of salt, loudness at 800 Hz, pitch at 5 or 40 dB, brightness, and possibly the sensation of temperature and auditory intensity discrimination (for a review see Holway and Pratt 1936; or Norwich 1993).

5.1.5 The Poulton-Teghtsoonian relation

The value $R = \left(\frac{N_0-1}{\gamma}\right)^{1/n}$ can then be conceived as the maximum perceivable intensity of a sensory modality. Indeed, beyond that value equation (5.22) becomes negative and has no physical meaning. Using then R as a measure of the stimulus range, the denominator of equation (5.22) implies the same relation found by Teghtsoonian (1971) working on data collected by Poulton (1967); that is, the range of sensation and the Stevens's exponent are inversely related:

$$n \log_{10} R = c_T \quad (5.24)$$

where c_T in literature is generally considered of the order $c_T \approx 2$ (Norwich 1993). In particular, Teghtsoonian's finding was $c_T \approx 1.53$.

Relation (5.24) can be derived from the weber fraction (5.22) by simply considering that the divergent value defined by the range R :

$$R^n = \frac{N_0 - 1}{\gamma}$$

implies:

$$n \log_{10} R = \log_{10} \left(\frac{N_0 - 1}{\gamma} \right)$$

that once taken:

$$c_T = \log_{10} \left(\frac{N_0 - 1}{\gamma} \right) \quad (5.25)$$

is exactly relation (5.24). Furthermore, the constant c_T is now related to the system's parameters N_0 and γ .

5.2 Fit to real data and discussion

In this section will be analyzed and discussed the fitting of equation (5.22) to some data taken from literature ³ and some flaws or shortcomings of the model that deserve to be marked. However, looking at the following results it must be kept in mind that the use of hypothesis (5.1) is a very strong approximation that, if energy (4.14) is used to model a nerve fiber, equates the energy-jnd to the single spike in the nerve.

5.2.1 Data of Lemberger on taste

A very famous set of data about the sense of taste was collected by Lemberger (1908) reporting the differential threshold of taste of sucrose against the concentration of the tasted solution. Fitting these data with equation (5.22) gives:

Quantity	Value	95%confidence bound	
N_0	29	(26, 32)	(5.26)
γ	0.20	(0.14, 0.26)	
n	1.1	(0.9, 1.3)	

Results of the fitting are plotted in figure (5.1):

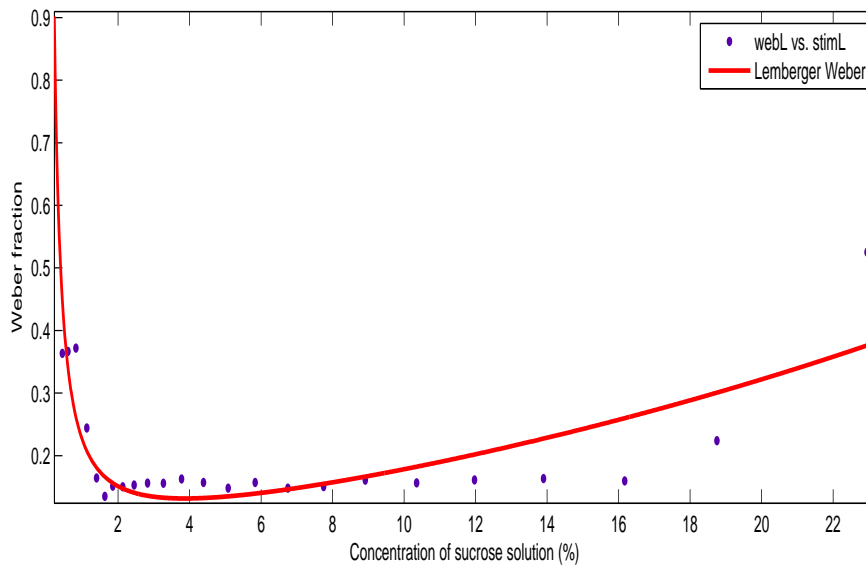


Figure 5.1: Data of Lemberger (1908) for differential threshold of taste of sucrose. Weber's fraction plotted against concentration of tasted solution.

with the following indexes of fit: $R^2 = 0.69$ and $RMSE = 0.06$.

In particular, with the values listed in (5.26), the resulting Teghtsoonian's constant (5.25) is $c_T = 2.13$ and the Weber ratio (5.23) is $k_W = 0.13$.

³The fits have been performed with the Nonlinear least squares using the MATLAB's *cftool*.

It is interesting to observe that all the quantities appear to be sensible from a physical point of view. Most of all, they have the same order of magnitude of those found experimentally. Indeed, the value of the Teghtsoonian constant is very close to the value of 2 usually considered in literature; the Weber ratio is very close to the literature's value of $k_W = 0.17$ (Baird and Noma 1978) and finally the exponent n agrees with the values that can be found in literature and that ranges between 0.6 and 1.30 (Baird and Noma 1978; Purg e 1995).

It must be notice however that the plateau of the experimental data appears to be greater than the one provided by equation (5.22). In particular, the rising slope of equation (5.22) is slower than the actual one.

5.2.2 Data of Oberlin on heaviness

A set of data about the differential threshold of heaviness was collected by Oberlin (1936). Fitting these data with equation (5.22) gives:

Quantity	Value	95%confidence bound	
N_0	222	(132, 313)	(5.27)
γ	0.73	(0.23, 1.24)	
n	0.75	(0.14, 1.36)	

Results of the fitting are plotted in figure (5.2):

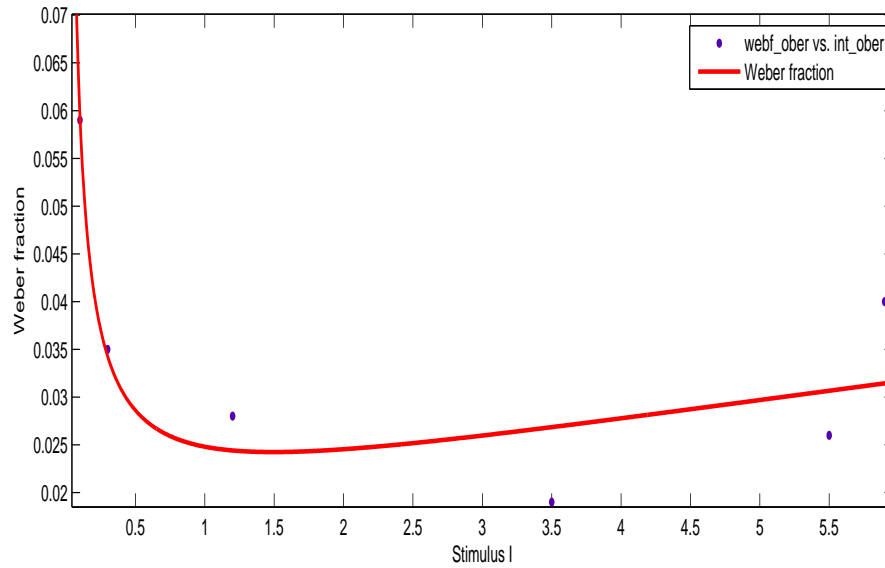


Figure 5.2: Data of Oberlin (1936) for differential threshold of heaviness. Weber's fraction plotted against weight (g).

with the following indexes of fit: $R^2 = 0.83$ and $RMSE = 0.01$.

In particular, with the values listed in (5.27), the resulting Teghtsoonian's constant (5.25) is $c_T = 2.5$ and the Weber ratio (5.23) is $k_W = 0.02$. Literature's values for the Weber ratio are usually around $k_W = 0.07$ while for the exponent n range between 1.1 and 1.45 (Baird and Noma 1978; Purg e 1995).

The agreement in between the 95% confidence bound can still be found, but it is clear that in this set of data, as in the previous one, both the rising slope is slower than the actual one and the minimum of equation (5.22) appears to precede the actual one, clearly failing in predicting the exact trend.

5.2.3 Data on skin indentation

Data of Kiesov

Data regarding the differential threshold for single skin indentation on the palm were recorded by Kiesov (data taken from Greenspan and Bolanowski 1996). Fitting these data with equation (5.22) gives:

Quantity	Value	95%confidence bound	
N_0	27	(21, 33)	(5.28)
γ	0.25	(0.14, 0.36)	
n	1.13	(0.74, 1.52)	

Results of the fitting are plotted in figure (5.3):

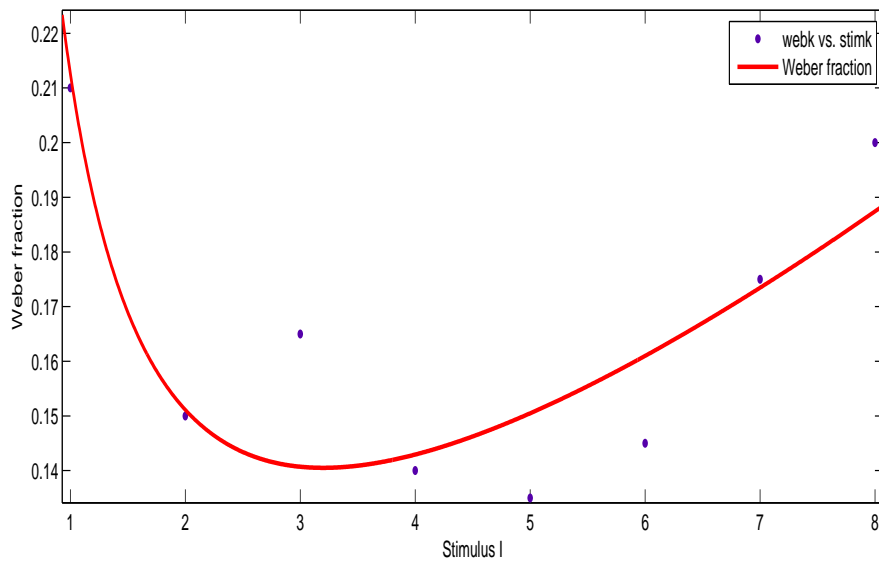


Figure 5.3: Data of Kiesov (Greenspan and Bolanowski 1996). Differential threshold of single skin indentation on the hand (tension: gr/mm).

with the following indexes of fit: $R^2 = 0.77$ and $RMSE = 0.02$.

In particular, with the values listed in (5.28), the resulting Teghtsoonian's constant (5.25) is $c_T = 2.02$ and the Weber ratio (5.23) is $k_W = 0.14$.

Data of Gatti and Dodge

Another set of data regarding the differential threshold for single skin indentation on the palm was recorded by Gatti and Dodge (data taken from Greenspan and Bolanowski 1996). Fitting these data with equation (5.22) gives:

Quantity	Value	95%confidence bound	
N_0	39	(32, 46)	(5.29)
γ	0.33	(0.28, 0.38)	
n	0.77	(0.61, 0.94)	

Results of the fitting are plotted in figure (5.4):

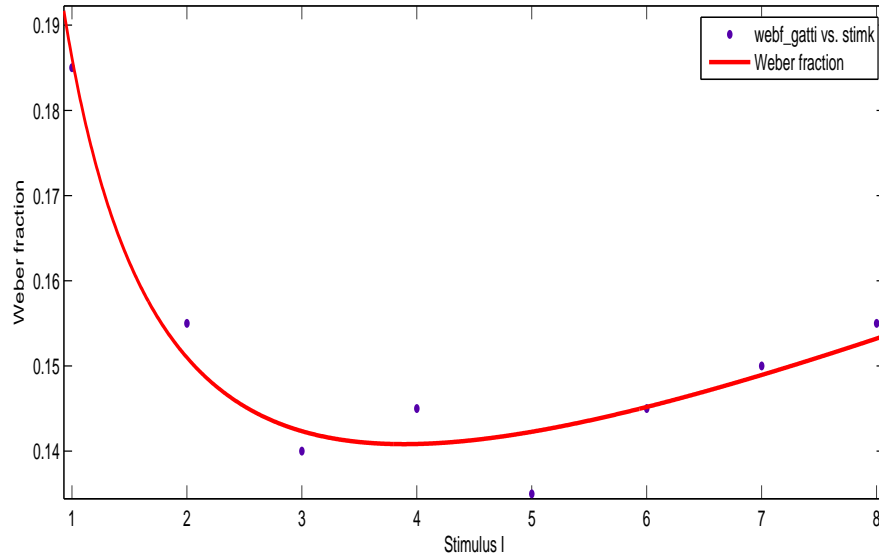


Figure 5.4: Data of Gatti and Dodge (Greenspan and Bolanowski 1996). Differential threshold of single skin indentation on the hand (tension: gr/mm).

with the following indexes of fit: $R^2 = 0.94$ and $RMSE = 0.004$.

In particular, with the values listed in (5.29), the resulting Teghtsoonian's constant (5.25) is $c_T = 2.1$ and the Weber ratio (5.23) is again $k_W = 0.14$.

Literature's value for the exponent n are usually around 1.10 (Purghé 1995) hence the agreement appears to be better with the data of Kiesow than with those of Gatti and Dodge. A slightly better fit that results also in a better value of the Teghtsoonian constant.

It is also interesting that, in both the previous data set on skin indentation as in those of Lemberger and Oberlin the rising slope is slower than the actual one. Moreover the minimum of equation (5.22) still appears to precede the actual one.

5.2.4 Differential threshold for brightness

An important set of data regarding the differential sensibility to brightness was recorded by König and Brodhun (see Hecht 1924). Fitting these data with equation (5.22) gives:

Quantity	Value	95%confidence bound	
N_0	651	(487, 815)	(5.30)
γ	3.98	(2.50, 5.46)	
n	0.37	(0.35, 0.40)	

Results of the fitting are plotted in figure (5.5):

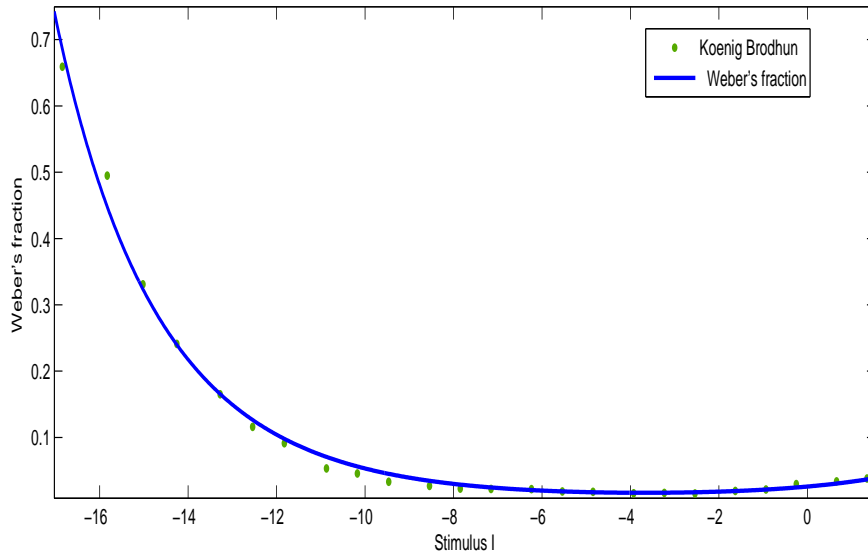


Figure 5.5: Data of König and Brodhun (see Hecht 1924). Differential sensitivity to brightness plotted against the intensity of the stimulus (Lamberts, logarithmic scale).

with the following indexes of fit: $R^2 = 0.99$ and $RMSE = 0.014$.

In particular, with the values listed in (5.30), the resulting Teghtsoonian's constant (5.25) is $c_T = 2.21$ and the Weber ratio (5.23) is again $k_W = 0.02$.

It is quite remarkable that, in spite of the fact that vision is a rather complex sense compared to touch and taste, the fit of equation 5.22 is very good. Moreover, considering that literature's values for the exponent n and the Weber ratio are usually around $n = 0.30$ and $k_W = 0.08$ (Baird and Noma 1978; Purghé 1995) the results can be considered quite good.

5.2.5 Data of Upton on loudness localization

An interesting set of data was collected by Upton (1936) for the binaural localization of a sound at 800Hz. When both ears are stimulated with the same energy the resulting apparent sound is localized in the median plane of the head. A shift of the energy on one ear implies a shift in the sound off the median plane. Fitting these data with equation (5.22) gives:

Quantity	Value	95%confidence bound	
N_0	84	(73, 95)	(5.31)
γ	2.1	(1.6, 2.6)	
n	0.62	(0.56, 0.68)	

Results of the fitting are plotted in figure (5.6):

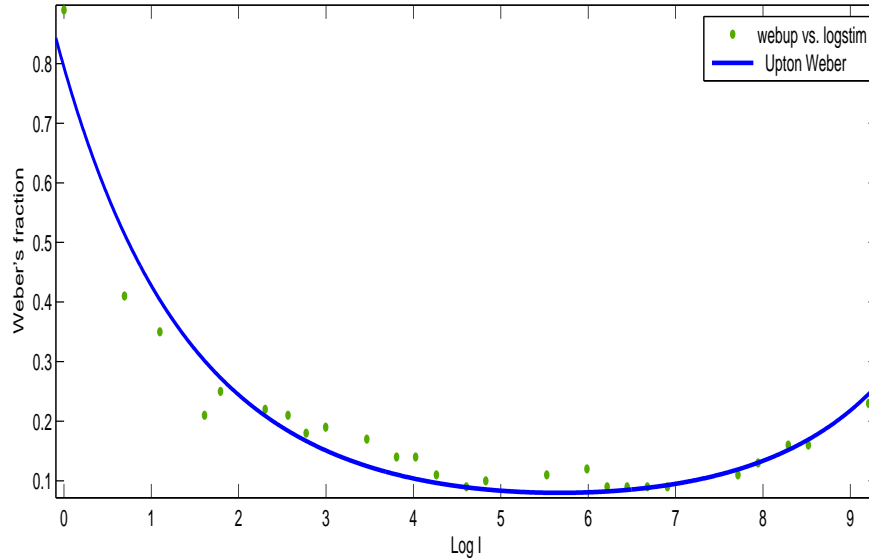


Figure 5.6: Data of Upton (1936), for the binaural localization of a sound at 800Hz. Differential sensitivity plotted against the logarithm of speakers' Voltage intensity (the relation between the electrical energy and the acoustic energy was linear).

with the following indexes of fit: $R^2 = 0.94$ and $RMSE = 0.04$.

In particular, with these values, the resulting Teghtsoonian's constant (5.25) is $c_T = 1.6$ and the Weber ratio (5.23) is again $k_W = 0.08$. Literature's values for the exponent n and the Weber ratio are usually around $n = 0.33$ (for frequency of 800Hz) and $k_W = 0.1$. The agreement can be considered quite good. In particular, considering that the exponent $n = 0.62$ listed in (5.31) has been obtained using as intensity a linearly measure of the acoustic energy it must be divided by two, since the sound pressure exponent is twice the sound intensity exponent (Baird and Noma 1978; Purghé 1995; Norwich 1993).

Finally, it is worthy of notice, that binaural localization is obviously a rather high level of perception, more complex than the previous cases and far more complex than the model developed in this thesis. Yet it is an interesting data set because, not only the resulting Weber fraction for binaural localization is of the type which commonly describe differential intensity sensitivity in animal (Upton 1936), but also because it shows an almost perfect fit of equation (5.22). This result strengthen the idea that a mechanical treatise could be of more general and abstract use since the choice of the nerve fiber's energy is just one out of several possibilities.

5.2.6 Discussion about the previous fits

The previous findings show, on the whole, a quite good agreement of equation (5.22) with data taken from literature. In particular, they exhibit a quite good agreement with the values of Weber's ratios and a discrete consistency with the value of Teghtsoonian's constant. Although some Stevens' exponents instead appear to be slightly overestimated or underestimated, they never deviate unduly from the range of the literature values⁴. Most of all, the general agreement can be considered acceptable since, in spite of the great deal of approximations that has been done, the magnitude of the parameters always suits the actual data.

Nevertheless, although from a qualitative point of view the trend of equation (5.22) appears to be very interesting and encompasses several known features of the Weber fraction, quantitatively it shows a couple of strong shortcomings: first, its minimum often occurs before the actual one, thus shifting the plateau's range in which the function could be approximated with a constant; second, its rising portion appears to increase more slowly than the actual data.

There could be several possible explanations for this behavior, but it must be kept in mind that Weber's fraction (5.22) has been derived using as energy equation (4.14) and then assuming, with hypothesis (5.1), the constancy of the energy-jnds along all the neuroelectric continua. These are two strong approximations to be made. First of all, equation (4.14) is not necessarily correct and most of all is not necessarily the best description of any neuroelectric behavior. Second, assumption (5.1) is a rather strong approximation of a behavior that actually could be a lot more complicated.

Indeed, there is an understood hypothesis behind all the previous work, that is the universality of the particular shape of equations (4.14) and (5.22) to describe the behavior of different sensory modalities. This is unlikely true. More likely, different laws should be used to describe each sensory modality, thus implying (in the context of the same variational framework) different shape of the Weber fraction. The latter indeed does not always shows an increasing terminal part: famous examples are visual and tactual length, finger-span, duration, temperature, and sound intensity detected by a single ear (Baird and Noma 1978; Norwich 1993; Coren et al. 1999).

Still, in our opinion the behavior of the fits can be considered quite good since the model appears capable of grasping the fundamental feature of many sensory modalities moving from general and abstract assumptions. Most of all, it appears interesting that the better fits are those pertaining the more complex cases of brightness and binaural localization. On one side this could be the result of their more smooth trends, on the other side it suggests that the statistical mechanical approach used in this chapter is a rather abstract methodology capable of dealing with higher level of sensation and perception.

Finally, it is worthy of notice that in the previous sets of data, the higher is the deviation from the actual value of the Teghtsoonian constant c_T the less precise is the estimation of all the other parameters. This happens because c_T connects all

⁴Values of Stevens' exponents of or Weber's ratios indeed can vary largely depending on the involved methods and procedures of measurement (See for instance Baird and Noma 1978; Stevens 1971; Geissler 1975; Purgé 1995)

the other quantities through the Poulton-Teghtsoonian relation (5.24).

Behavior of the model at the range R

It is worthy to analyze the behavior of the model as the intensity I approaches the value R . The same divergence of the Weber fraction can indeed be seen in the generalized jnd. Equation (5.19):

$$\Delta\psi = k \log \left(\frac{1 + \gamma w(I)I^n}{1 + \gamma I^n} \right)$$

can be rewritten, using the value of w given by:

$$w(I) = \left(\frac{\frac{1}{\gamma} + (N_0 + 1)I^n}{N_0 - (1 + \gamma I^n)} \right) \frac{1}{I^n}$$

as:

$$\Delta\psi = k \log \left(\frac{N_0}{N_0 - (1 + \gamma I^n)} \right)$$

that is physically meaningful only for $I \in [0, R]$. That is, like the Weber fraction (5.22), shows a divergence at $I = R$.

In addition, the psychophysical law at $I = R$ takes the value:

$$\psi(R) = k \log \left(\frac{1 + \gamma \frac{N_0 - 1}{\gamma}}{1 + \gamma I_0^n} \right) = k \log N_\infty$$

thus relating the maximum value of sensation to the maximum number of energy jnds that can be accumulated (or the number of spikes if the energy is used to describe a nerve fiber).

Instead the effective number of energy-jnds given by equation (5.5) is:

$$N_P(R) = N_0 \frac{\gamma \left(\frac{N_0 - 1}{\gamma} - I_0^n \right)}{(1 + \gamma \frac{N_0 - 1}{\gamma})(1 + \gamma I_0^n)} = N_\infty - 1$$

and corresponds to an energy value of:

$$E(R) = \epsilon(N_\infty - 1)$$

the saturation then occurs only in the last energy-jnd, beyond the upper threshold value, where equation (5.22) has no physical meaning, so the system does not perceive stimuli that correspond to the saturating part of the neuroelectric response.

These findings are obviously arguable and open to debate, but very interesting.

Furthermore, these results could be mainly due to the approximations introduced that force the model to cope with singularities at the value R . Perhaps,

simply relaxing some of the strong assumptions that have been made could allow for improvement; one above all, hypothesis (5.2): a generalization like $\Delta E(I)$ indeed would introduce further terms in equation (5.22) and in the other quantities.

5.3 Summary

In this chapter statistical mechanics has been introduced to account for both the limited resolving power of the psychophysical systems and the discreteness of many sensory modalities. In particular, it has been posited that the perceiving system is not capable of discriminating between different sensations whose neurelectric energies are very close to each other. Moving from this assumption and using the shape of the energy modeled in chapter four some laws of psychophysics have been derived: the Bloch-Charpentier Law (or equivalently the Weiss-Lapicque law in the case of irritable tissues), the Ekman law and a general shape for the jnd, the Poulton-Teghtsoonian relation and finally a shape of the Weber fraction capable of accounting for the decreasing trend at low intensities and the rising portion close to the end of the perceiving range.

The Weber fraction, in particular, have been tested on data taken from literature on the discrimination of sucrose concentration, heaviness, brightness, loudness and skin indentation, revealing a discrete agreement but also some shortcomings. In particular, its minimum appears to anticipate the actual one systematically, making then the rising portion to increase more slowly than the actual data.

Chapter 6

An extension to time

In this chapter we will sketch an extension of the model developed in the previous chapters to the case of time-varying stimuli. This is not a complete treatise but just the preliminary results of a possible extension.

6.1 Time-varying stimulus

If the stimulus is allowed to vary in time, the variation of psychophysical law is:

$$\dot{\psi} = \frac{\partial \psi}{\partial I} \dot{I} + \frac{\partial \psi}{\partial t} \quad (6.1)$$

Hence, if we hypothesize that the system is still following a Lagrangian like (3.9) we could expect the energy to be something similar to:

$$H_P = \frac{\Pi}{2} \left(\frac{\partial \psi}{\partial I} \dot{I} + \frac{\partial \psi}{\partial t} \right) = H_I + H_t \quad (6.2)$$

that is the sum of a first term, related to the variation of sensation respect to the intensity, and a second term related to the variation of sensation respect to the time. However, this simple generalization introduces some difficulties.

First, in the steady stimulus situation the trend of psychophysical law was due to the only adaptation hence it was a decreasing one, implying that Π was less than zero by keeping m greater than zero in Lagrangian (3.9). Instead now the momentum Π must be constant independently on possible switches from positive to negative value of $\dot{\psi}$. Hence the modulating function m must be allowed to take both positive and negative values. Does that mean that the energy can take both positive and negative value? What is the meaning of a negative firing rate?

Second, in the steady stimulus situation it was impossible to have a constant perception. Instead now, it is sufficient to take a stimulus that varies in the opposite direction of adaptation to keep sensation constant, that is:

$$\dot{I} = -\frac{\partial \psi}{\partial t} / \frac{\partial \psi}{\partial I} \quad (6.3)$$

But in such a case the energy would be equal to zero. Does that mean that the firing rate is equal to zero?

As an example of this ill behavior, let us take the case of null threshold, $I_0 \rightarrow 0$, and $r = 1$, just to simplify the psychophysical law (4.13):

$$\psi = k \log \left(1 + \beta \frac{I^n}{t} \right)$$

Which corresponds to an energy¹:

$$H = \frac{\Pi}{2} \dot{\psi} = \frac{\Pi}{2} \frac{k\beta}{t(t + \beta I^n)} \left(\frac{n\dot{I}t}{I} - 1 \right) \quad (6.4)$$

Hence a stimulus that increases in time like $I(t) = ct^{1/n}$ results in a constant psychophysical law and in a null value of the energy. Does this mean that in the case of a nerve fiber the firing rate goes to zero?

6.1.1 Possible interpretations

The first thing that must be noticed about the structure of the Hamiltonian (6.2) is that it appears to describe an interplay between two terms that act like a sort of excitatory-inhibitory mechanism leading to perception. For instance, let us consider a stimulus that increases and then reaches a steady state. In equations (6.2) and (6.4) there are a positive term and a negative term²: the first one, H_I , follows the variation of the stimulus, $\frac{\partial \psi}{\partial I}$, and leads the equation during the initial phases of stimulation, while the second one, H_t , follows the adaptation, $\frac{\partial \psi}{\partial t}$, and leads the system during the steady phase. Then, is it still sensible to interpret the Hamiltonian H_P as a measure of the firing rate?

There are two possible solutions: first, if both H_I and H_t were measures of firing rates then H_P could not be a measure of the *total* firing rate, since the quantities do not necessarily sum up. Second, if H_P were instead a measure of the *total* firing rate then H_I and H_t couldn't be measures of firing rate too.

So, if Hamiltonian H_P were not a measure of the *total* firing rate but only of a sort of *clean* part of it that is dedicated to perception, the two terms on the right side of Hamiltonian (6.2) might be, for instance, a measure of two separated trains of spikes. In a similar case they would sum up to give the total firing rate:

$$|H_I| + |H_t| \rightarrow f = f_I + f_t \quad (6.5)$$

¹It must be noticed that equation (6.4) is a Naka-Rushton relation modulated by the variation of the stimulus intensity, $I(t)$. It also straightforward that, in a steady stimulus situation, $\dot{I} = 0$, since the Π becomes negative, equation (6.4) becomes exactly (4.4).

²Actually it must be noticed that both the terms could be negative if the stimulus were decreasing, $\dot{I} < 0$. Nevertheless, in order to decrease a stimulus must have increased before so that there have must been a phase in which the first term was positive, thus accumulating step by step a positive energy by which starting to decrease the value.

but the structure of H_P would be the description of an interplay between an excitatory and an inhibitory mechanisms that leads to perception. That is, a *clean* firing rate related to the energy behind behavior. For instance, there could be a part related to excitatory nerve fibers and a part related to inhibitory nerve fibers, their clean result would be the energy used to achieve the final action or perception (Kandel et al. 2000).

This is a simple interpretation yet, while it is not difficult to apply it to a multichannel system, since the inhibitory and excitatory parts can be seen as the result of two different processes related to different physiological parts, what would happen in a single channel, like a single unit or nerve fiber?

In that case, existing only one physical device it would be impossible to talk about two or more different trains of spikes. A more suitable interpretation would be the second one where H_P measures the resulting firing rate and the excitatory-inhibitory mechanism is achieved in different ways, like in the synaptic behavior.

This interpretation simplifies the problems brought up in the previous section, but still does not explain how the energy H_P (and thus the firing rate) could be positive, negative or null. In order to try to give an explanation we need to consider two different situations: the presence and the absence of spontaneous activity.

6.1.2 Presence of spontaneous activity

It must be noticed that, without changing its solutions, Lagrangian (3.9) can be changed by simply adding a time dependent term³:

$$\tilde{L} = \frac{1}{2}m(I(t), t)\dot{\psi}^2 - A(t) \quad (6.6)$$

with the corresponding Hamiltonian:

$$\tilde{H} = \frac{\pi^2}{2m(I(t), t)} + A(t) \quad (6.7)$$

In particular, then:

$$\tilde{H} = \frac{\pi}{2}\dot{\psi} + A(t) \quad (6.8)$$

whenever sensation were constant, energy would be not necessarily equal to zero, but could still be described by some on-going or spontaneous activity $A(t)$. Indeed, from this point of view, the model of energy discussed in the previous chapters was cleaned by the effects of a spontaneous or resting activity, as we noticed in section (4.2.1). This would be like a shift of the energy that does not change the properties of the system but it changes the interpretation of the relation between

³Actually this result is a consequence of the gauge's invariance discussed in section (1.1.4). In this case indeed $A(t)$ behaves like the time derivative of a function $F(\psi, t)$ that is a total derivative of time. A more general result would be to take a new Lagrangian like: $\tilde{L} = cL + \frac{d}{dt}F(\psi, t)$ where the function F could also be a function of ψ thus introducing the dependence on the magnitude of sensation but without affecting the conservation of momentum Π .

firing rate and sensation given in section (4.1.1). Indeed, changes in time of the sensation, $\dot{\psi}$, would be related to the changes in firing rate in comparison to the baseline, $f(I(t), t) - A(t)$. In particular the changes in firing rate respect to the baseline could be both positive or negative. This seems to parallel electrophysiological findings on primates that shows how, in several senses, conscious perception is related to small local consumption of energy due to variations in the mean cortical neuron firing rate that can be both positive or negative (Schölvink et al. 2008).

6.1.3 Absence of spontaneous activity

In the absence of spontaneous activity, or in the presence of a negligible term $A(t)$ in the Lagrangian (3.9), the changes in $\dot{\psi}$ can lead the Hamiltonian H_P to take both positive and negative values.

This result appears to be paradoxical since a negative firing rate does not have any physical sense. Nevertheless, in the model that we have developed in the previous chapters the sensation appears to be an accumulation of energy during the rising phase of the stimulus, like an addition of excitation to excitation, while adaptation behaves like a negative feedback that reduces the total amount of energy. The sign of the energy appears then to be only an indication of the fact that energy must be increased or decreased, but the physiological correspondent is given by the module of the energy that is by definition a positive quantity.

In detail, during the rising phase of the stimulus the system behaves like a counter that reads the number of spikes travelling inside the nerve and accumulates them in a sort of memory that quantifies sensation. Then a sort of switch is activated and the system, still counting the spikes travelling inside the nerve, uses their number to reduce the amount of energy previously stored in memory. Yet the physiological background is the same.

As an example, let us consider an increasing stimulus that reaches a certain value and then it becomes steady. The correspondent sensation increases up to a maximum value and then starts to decrease following adaptation. What is the pattern followed by the firing rate under the hypothesis of this model?

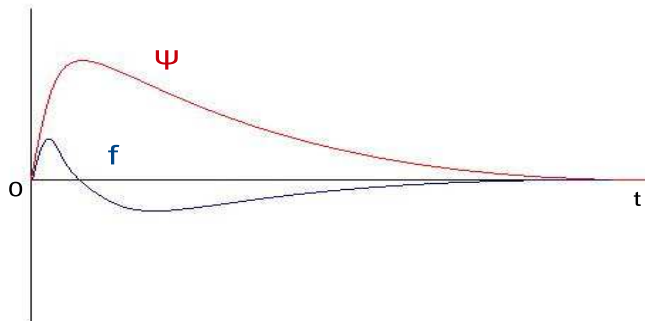


Figure 6.1: Trajectory followed by sensation and firing rate.

As in figure (6.1), firing rate increases up to a maximum and then it decreases attaining a zero value at the same intensity at which the sensation attains its maximum. After that it continues on a negative scale reaching a minimum and then raising up to zero (asintotically since we are considering the limit $t \rightarrow \infty$), the latter phase corresponding to the adapted state of sensation.

This is a particularly interesting result, because if we consider only the magnitude of the firing rate we have a first train of spikes, corresponding to the dynamic part of the stimulation, after which we have a pause in the firing, corresponding to the maximum of sensation, and then we have a longer second train of spikes corresponding to the static part of sensation.

This behavior is quiet common and can be easily seen, for instance, in the neur-electric response of primary muscle spindles or in slow adapting mechanoreceptors (Knibestöl 1975; Katz 1950; Matthews 1931; Nudelman and Agarwal 1972).

6.2 Examples of time varying systems

In this section are given some examples of time-varying stimuli. In particular, the first one is an Heaviside function to represent a steady stimulus abruptly rising while the second is an exponential increasing stimulus up to a steady value.

6.2.1 Heaviside function

The Heaviside function is defined as the function that attains the null value except for an interval in which attains the a constant value. In particular then:

$$I(t) = I_M H(t - t_0) \quad (6.9)$$

represents a stimulus that does not exist before the instant $t = t_0$ and after which it attains the value I_M . In particular its derivative depends on the derivative of the Heaviside function:

$$\dot{I}(t) = I_M \delta(t - t_0) \quad (6.10)$$

where δ is the Dirac delta that attains the null value everywhere except than in $t = t_0$. The associated psychophysical law⁴ will be:

$$\psi = k \log \left(1 + \frac{\beta I_M^n}{t} \right) \quad (6.11)$$

for $t \geq t_0$, and zero before. So the sensation arises abruptly. The first derivative, and hence the firing rate will then be:

$$f = \frac{\Pi k}{2h} \frac{\beta I_M^n}{t(t + \beta I_M^n)} \left(\frac{nt\delta(t - t_0)}{I_M} - 1 \right) \quad (6.12)$$

⁴It has been chosen to use equation (4.13) with $r = 1$ and $I_0 \rightarrow 0$ instead of equation (4.10) for sake of simplicity.

So that the number of action potential released in an interval (t_0, ∞) is:

$$\Delta N = \int_{t_0}^{\infty} f dt' = \frac{\Pi k}{2h} \left[\frac{n\beta I_M^{n-1}}{t_0 + \beta I_M^n} + \log \left(\frac{t_0}{t_0 + \beta I_M^n} \right) \right] \quad (6.13)$$

where the first term is the number of spikes generated during the rising phase, that is the first train of spikes, while the second term is the number of spikes generated during the static stimulation.

6.2.2 Increasing stimulus

A fast increasing stimulus, up to a certain value I_M , can be modeled as:

$$I(t) = I_M(1 - \exp(-\frac{t}{\tau})) \quad (6.14)$$

that has the first derivative:

$$\dot{I}(t) = \frac{I_M}{\tau} \exp(-\frac{t}{\tau}) \quad (6.15)$$

The corresponding psychophysical behavior (4.13) is:

$$\psi = k \log \left(1 + \frac{\beta I_M^n (1 - \exp(-\frac{t}{\tau}))^n}{t^r} \right) \quad (6.16)$$

It is interesting to see that, in the limit of $t \rightarrow 0$, a Taylor expansion gives:

$$\psi \approx k \log \left(1 + \frac{\beta I_M^n}{\tau} t^{n-r} \right) \quad (6.17)$$

So that, when the exponent n of the psychophysical law is greater than the exponent r that leads the dynamic range adaptation, the sensation increases moving from zero up to a maximum and then decreasing. Hence the firing rate behaves as hypothesized in section (6.1.3) and depicted in figure (6.1). There a first train of spikes, then a pause, and then a second train of spikes.

6.3 Summary

In this chapter the model developed in the thesis has been extended to time-varying stimuli and to the addition of a spontaneous or resting activity. As a result, the behavior of the firing rate corresponding to a stimulus that increases and then becomes steady shows an initial burst, followed by a pause and then a longer train of spikes that follow the static stimulation. A behavior that has been found in several experiments.

Chapter 7

Discussion and conclusions

The main idea suggested in this thesis is that, if in an abstract model the process of perception were described as a pattern in time, then its Hamiltonian could be related to neurophysiological features. In particular, being the Hamiltonian the energy possessed by the process, and hence needed to sustain it, it could be related to metabolic or neurelectric features.

Hence, variational calculus, with a particular focus on the methods of analytical mechanics, has been applied to perception and psychophysics considering the psychophysical law as the solution of an Euler-Lagrange equation. In particular, the pattern followed by sensation during the psychophysical adaptation to a steady stimulus has been chosen as the solution of the motion equation.

The Lagrangian function, (3.9), chosen in the third chapter to summarize the system's behavior while allowing to obtain the classical psychophysical laws, is very simple: changes in sensation are described as a free particle motion with a variable mass. In spite of its particular shape, this Lagrangian shows several interesting properties: first of all, it is a sufficient but not a necessary condition; second, its structure is needed by the Noether's theorem to ensure the measurability of the psychological continua on an interval scale; third, it depicts the process of perception as a process layered over other processes and completely driven by them. Finally, the energy of the system is not conserved.

This latter feature, in particular, since energy during the adaptation phenomenon depletes in time, could be considered as a reduction of the metabolic costs and be tentatively connected with neurophysiological aspects. For instance, spike frequency adaptation in single units or depletion of the whole electrical activity in afferent nerves are well known to parallel psychophysical adaptation, although in general with different time-scales (Diamant et al. 1965; Greenspan and Bolanowski 1996). Similar results hold for the discharge rate of neurons populations.

Furthermore, the model describes sensation as an integration in time of the energy, in a similar way that jnds are accumulated in psychophysics. In particular, the adaptation phenomenon behaves like a negative feedback: energy is used as a suppressor integrator to reduce the amount of previously accumulated sensation. Moreover, changes in sensation during an interval of time obey a stationarity principle, being the minimum or the maximum possible.

The knowledge of the shape of the energy then allows one to describe the system's behavior. As a working example in the fourth chapter an approximate shape

for the energy has been modeled on the Naka-Rushton relation (Naka and Rushton 1966) with the addition of some temporal features like spike frequency and dynamic range adaptation (Wen et al. 2009). The resulting energy (4.14) has been applied to a rough and simplified model of nerve fiber, showing some shortcomings but also some interesting results. First, neural adaptation appears indeed to follow an optimization principle: spike frequency adaptation occurs minimizing the total electrical activity, that is the system adapts using the minimum possible number of action potentials. Second, the velocity of the signal in the nerve is constant independently on the frequency of the signal. Third, neural adaptation occurs faster than psychophysical adaptation, and the electrical activity is used to reduce the sensation like a negative feedback. In particular, since the variable mass of the system becomes a measure of the inter-spike interval (ISI), spike frequency adaptation becomes the physiological process that drives psychophysical adaptation. Fourth, temporal adaptive features appear to link a saturating firing rate in primary afferent units with a psychophysical response that can range from a power law to a logarithmic law depending on the signal-to-noise ratio of the system. In particular, the resulting psychophysical law (4.10) is a further generalization of a law proposed by Delbouf and Helmholtz (Murray 1993) and derived by Norwich (1993) moving from Shannon's information entropy.

In chapter four the resulting equations for the psychophysical law (4.10) and for the neural response (4.15) have been applied to data taken from literature on the senses of touch and taste, with a particular focus on the former one. Touch can indeed be considered the simplest sense and hence the more suitable to a treatise that relates the energy of perception to the response of primary afferent units.

The results of the fitting suggests a good agreement of the model with the actual data. In particular, the psychophysical and the neural exponents obtained with the equations provided by the framework appear to be close to each other. This is an interesting result, since in literature neural exponents obtained with a power law are approximately the two third of the psychophysical law exponents obtained with magnitude estimation method (Krueger 1989; Murray 1993; McKenna 1985) but many authors (Stevens 1970; Barlow 1972) posited a linearity between them.

Other results of the model have been achieved in chapter five where, once introduced the concept of energy-jnd that implies a limit in the resolution of the perceiving systems, several empirical laws of psychophysics can be derived from the fundamental equations of the framework. In detail, The Bloch-Charpentier's law (5.8) and its generalizations (as like the Weiss-Lapicque law for the excitability of tissues), the Eikman's law and a generalization of the classical jnd (5.19), the Poulton-Teghtsoonian relation (5.24) between the extension of the perceptual range and Stevens' exponent; and finally a shape of the Weber fraction (5.22) capable of accounting, with a quite good approximation, for the deviations at the extremes of the perceiving range (a derivation of the Piéron law for simple reaction time is also given in the Appendixes).

Finally, a possible extension of the model to time-varying stimuli has been sketched in chapter six, leading to a preliminary result that could explain a quite typical pattern of discharge: namely, strong burst during dynamic stimulation, followed by a pause and then a longer and slower discharge pattern.

Nevertheless, notwithstanding the results achieved, it must be stressed that the

model shows several shortcomings and limits to its application:

1. First of all, the choice of Lagrangian (3.9) in chapter three is in a certain way arbitrary, since different Lagrangians can lead to the same motion equations (yet generally showing different properties). In particular there is an entire class of Lagrangians having similar properties, as it is stressed in the Appendixes. Moreover, it could be argued that Lagrangian (3.9) has its solution already built into it, since once one has set the function m any psychophysical law ψ can be derived. Possible answers to this argument have been given in chapter three. In particular, the choice of the shape (3.9) has been based on a parsimony principle: it is the simplest one that shows many features characterizing perception. Most of all, it must be remarked that it is a sufficient and not a necessary condition, hence better choices could always be possible.
2. Second, energy (4.14), developed in chapter four, is just an approximation built in a *bulk* condition in which adaptation is depleted to extinction and spontaneous activity is not considered; thus, neither it accounts for any possible adaptation trend nor for any possible stimulus-response curve. In addition, it becomes singular taking the limits $I_0, t \rightarrow 0$ thus revealing a limit of the boundary conditions chosen.
3. Third, the assumptions made to introduce both spike frequency adaptation and dynamic range adaptation into the Naka Rushton equation are rough compared to the actual behavior of a nerve (Dean et al. 2005; Wen et al. 2009). Similarly rough can be considered the hypothesis (5.1) of a constant energy-jnd introduced to limit the resolving power of the system. Yet the stronger are these hypotheses the more interesting appears to be the quite good fit obtained with actual data.
4. Fourth, but not less important, the hypothesis of linking the energy of the nerve fiber's electrical activity to the energy that underpins the psychophysical response is a strongly debatable simplification, since it cuts away all the processes between primary afferent units and the sensation that should be based on the activity of populations of neurons. The latter, indeed, is generally unrelated to the single neuron's response, particularly when the population is not homogeneous (Jakson 1974; Gerstner and Kistler 2002). Furthermore, a similar hypothesis does not account for the presence of peripheral activity without a corresponding behavioral correlate (McKenna 1985) or the diffusion of the neural code performed to minimize energy (Attwell and Laughlin 2001). Nevertheless, at least for the sense of touch can be considered an acceptable approximation. Moreover, positing a proportionality between psychophysical law and neuroelectric response, as it has been done by the sensory transducer theory (Stevens 1970) and the neuron doctrine (Barlow 1972), echoes the De Valois's idea of a *lower envelope* or *most sensitive neuron*, so that the system follows the channel with the highest signal-to-noise ratio (Barlow 1972). This idea, sometimes in slightly different shapes, has been proposed in various theories of conscious perception to solve the

so-called binding problem. Moreover, it could be corroborated by the experimental evidence that awareness seems to correlate with single-neuron activity (Rees et al. 2002).

In conclusion, although the model exhibits several shortcomings that need to be further investigate, and additional work is needed to encompass other behavioral or neuroelectrical laws, or to predict new phenomena, it appears fascinating that neural and psychophysical laws could be related by the general and abstract principles of variational calculus. Considering indeed the strong assumptions that have been done, still this model of perception based on optimization assumptions gives a good qualitative (and a discrete quantitative) description of both psychophysical and neuroelectric phenomena.

Appendix A

Stimulus as an independent variable

In section (2.2.2) it has been suggested that a possible approach to the use of Lagrangian in psychophysics could follow an equation like (2.12), considering the psychophysical function as a function of the only stimulus intensity, $\psi(I)$. The use of variational calculus respect to the stimulus intensity I leads then to a Lagrangian of the form $L(\psi, \psi', I)$ where ψ' is the first derivative of ψ respect to I , with associated Euler-Lagrange's equation:

$$\frac{d}{dI} \frac{\partial L}{\partial \psi'} - \frac{\partial L}{\partial \psi} = 0 \quad (\text{A.1})$$

which solution is the psychophysical law itself $\psi(I)$. Then the conjugate momentum is defined as:

$$\Pi \equiv \frac{\partial L}{\partial \psi'}$$

for an Hamiltonian defined as $H = \Pi\psi' - L$, such that:

$$\begin{cases} \psi' = \frac{\partial H}{\partial \Pi} \\ \Pi' = -\frac{\partial H}{\partial \psi} \end{cases}$$

In particular, for classical psychophysics, in order to have the measurability of the psychological continua on an interval scale we could ask, as in section (2.2.3), for the Lagrangian to have a shape like:

$$L(\psi, \psi', I) \equiv L(\psi', \psi) \quad (\text{A.2})$$

So the simplest choice is similar to Lagrangian (3.9):

$$L(\psi', I) = \frac{1}{2}m(I)\psi' \quad (\text{A.3})$$

It must be noticed however that Lagrangian (A.2) is a member of the general class of Lagrangians with a shape like $L(\psi', I) = \psi' f(\psi', I)$ where $f(\psi', I)$ is any function of ψ' and I . This class shares the fundamental result of the conservation of momentum $\Pi = f(\psi', I) + \psi' \frac{\partial f}{\partial \psi'}$ and has an Hamiltonian $H = \psi'^2 \frac{\partial f}{\partial \psi'}$.

For instance, another member of the same class, that also gives the same Euler-Lagrange equation, is: $L(\psi', I) = \psi' \log(m(I)\psi')$ that curiously resembles the Kullback-Liebr entropy. Obviously, different shape of $f(\psi')$ lead in general to different trends of the energy.

Equation (A.2), in particular, gives for the Fechner law:

$$m(I) = I \rightarrow \psi = \log I \rightarrow H = \frac{1}{I} \quad (\text{A.4})$$

while for Stevens' law gives:

$$m(I) = I^{1-n} \rightarrow \psi = \frac{I^n}{n} \rightarrow H = \frac{1}{I^{1-n}} \quad (\text{A.5})$$

and for the Delbouf-Helmoltz law:

$$m(I) = \frac{1 + I^n}{I^{n-1}} \rightarrow \psi = \log(1 + I^n) \rightarrow H = \frac{I^{n-1}}{1 + I^n} \quad (\text{A.6})$$

the latter in particular is very interesting since depending on the value of n can describe different trends.

Finally, it is important to notice that a similar approach to the psychophysical law does not always give the same results of the time approach used in the thesis. In particular, the energy related to the Delbouf-Helmoltz energy is not a Naka Rushton relation but a slight correction of it.

This suggests some interesting considerations: first, an approach completely without time could be useful for studying those systems that do not show adaptive phenomena. Hence, in those systems the relation between firing rate and sensation could be completely different from the result obtained in the thesis where adaptive phenomena play a fundamental role. Second, the absence of time can be considered equivalent to a constant time situation. Hence, the approach just used can be seen as a subcase of the time-varying stimulus approach depicted in chapter six: in particular, it is equivalent to study the partial derivative $\frac{\partial \psi}{\partial I}$ in equation (3.2), that is the dependence of the system by the stimulus taking the time constant.

Appendix B

Deepenings on equation (3.9)

B.1 An equation for Fechner's and Stevens' laws

Extending to time Fechner's and Stevens' laws gives:

$$\psi_F = k_F \log h(t) , \quad \psi_S = k_S h(t)^n$$

where $h(t) \equiv h(I(t), t)$ generalizes the psychophysical law's argument to be a function of time.

It is straightforward to verify that the previous equations can be common solutions to the same second order differential equation:

$$\ddot{\psi} = \left[(n-1) \frac{\dot{h}}{h} + \frac{\ddot{h}}{\dot{h}} \right] \dot{\psi} \tag{B.1}$$

in particular, the Stevens' solution can be obtained for any $n > 0$, while the Fechner's solution holds in the limit $n \rightarrow 0$. Thus, the latter holds in the limit in which the former becomes a constant since the exponent approaches zero (Krueger 1989). It is also important to stress that equation (B.1) is not the only equation that gives either the Fechner law or the Stevens law as solutions, but it is the one that gives both of them.

B.2 Derivation of equation (3.9)

Considering then as a general shape for the Lagrangian a linear combination of ψ and $\dot{\psi}$:

$$L(\psi, \dot{\psi}, t) = \frac{1}{a} A(t) \psi^a + \frac{1}{b} B(t) \dot{\psi}^b$$

where $a, b \in \mathbb{R}^+$, and the coefficients $A(t) \equiv A(I(t), t)$ and $B(t) \equiv B(I(t), t)$ may in general depend on time and stimulus intensity. For such a Lagrangian the associated Euler-Lagrange equation is:

$$\ddot{\psi} = \frac{A(t)\psi^{a-1}}{B(t)(b-1)}\dot{\psi}^{2-b} - \frac{\dot{B}(t)}{B(t)}\frac{\dot{\psi}}{b-1} \quad (\text{B.2})$$

with $b \neq 1$ and $B(t) \neq 0$. Equations (B.1) and (B.2) are the same if the coefficients:

$$A(t) = 0 \quad , \quad B(t) = \left(\frac{h^{1-n}}{\dot{h}} \right)^{b-1} \quad , \quad b \neq 1$$

Hence a generalization of Fechner's and Steven's law can be obtained by the family of Lagrangians:

$$L = \frac{1}{b}B(t)\dot{\psi}^b$$

Applying Legendre's transformation (3.8), Hamiltonian can be easily found and rewritten in the state space coordinates $(\psi, \dot{\psi})$:

$$\mathcal{H}(\psi, \dot{\psi}, t) = \left(\frac{b-1}{b} \right) B(t) \dot{\psi}^b = (b-1)L(\psi, \dot{\psi}, t)$$

that actually is the Lagrangian unless of a scaling term. So, Hamiltonian and Lagrangian appear to differ only for a ratio scaling term. Asking that $\mathcal{H} = L$ gives without loss of generality $b = 2$. Renaming then $B(t) = m(I(t), t)$ and considering a steady stimulus situation $I(t) \equiv I$ gives exactly the Lagrangian (3.9).

B.2.1 Other possible Lagrangians

It must be noticed that the absence of any dependence on ψ in the previous Lagrangian is equivalent to require a Lagrangian like $L(\dot{\psi}, t)$ in order to have the measurability on interval scale of the sensation continuum, as stated by Noether's theorem. In addition, a more general solution for the Lagrangian could be searched in the form of a power series like:

$$L(\dot{\psi}) = \sum_k a_k(t) \dot{\psi}^k$$

it is straightforward to see that, except for the term $a_0(t)$ that does not alter the Lagrangian and is equivalent to the addition of a resting activity as discussed in chapter six, the only surviving term in order to have equation (B.1), is $a_2(t)$ corresponding to $k = 2$, that is the quadratic term previously used.

Obviously, a Lagrangian could be chosen among the transcendental functions. For instance, as it has been already noticed in Appendix A, equation (3.9) can also be given by any Lagrangians of the kind:

$$L(\dot{\psi}, t) = \dot{\psi} f(\dot{\psi}, t) \quad (\text{B.3})$$

where $f(\dot{\psi}, t)$ is any function of $\dot{\psi}$ and t . This class shares the fundamental result of the conservation of momentum:

$$\Pi = f(\dot{\psi}, t) + \dot{\psi} \frac{\partial f}{\partial \dot{\psi}} \quad (\text{B.4})$$

and has an Hamiltonian:

$$H = \dot{\psi}^2 \frac{\partial f}{\partial \dot{\psi}} \quad (\text{B.5})$$

For instance, a member of this class, that also gives the same Euler-Lagrange equation of (3.9), is:

$$L(\dot{\psi}, I) = |\dot{\psi}| \log |m(I, t)\dot{\psi}| \quad (\text{B.6})$$

that resembles the Kullback-Liebr entropy. Obviously, different shape of $f(\dot{\psi})$ lead in general to different trends of the energy. Nevertheless, among all these possibilities still equation (3.9) appear to be the simplest one.

Appendix C

Model of nerve

Let us consider a very simplified model of nerve fiber approximated a by tube of section πr^2 and with a distance between the Ranvier nodes of d_R .

Independently on the presence or absence of the adaptation phenomenon the motion of a train of spikes is related to a liquid wave travelling inside the axon. Indeed the spikes is generated by an exchange of ionic currents due to the action of ion pumps (Kandel et al. 2000). In particular, since there's a continuous exchange, particularly at the Ranvier nodes, the resulting total density can be considered a function of time. So the resulting density of kinetic energy can be written as:

$$\epsilon(t) = \frac{1}{2}\rho(t)v^2 \quad (\text{C.1})$$

where the velocity v is a constant and measures the velocity at which the perturbation in the ionic density (that is the signal) is travelling.

On the other side, the energy (3.13) of the system can be rewritten as:

$$E = \frac{1}{2}m(I, t)\dot{\psi}^2 \quad (\text{C.2})$$

that, using the equivalences given in section (4.1.1), becomes:

$$E = \frac{1}{2} \left(\frac{\Pi^2}{2hv} \lambda(I, t) \right) \left(\frac{2h}{\Pi} f \right)^2 \quad (\text{C.3})$$

and simplifying:

$$E = \frac{1}{2} \left(\frac{2h}{v\lambda(I, t)} \right) (\lambda f)^2 \quad (\text{C.4})$$

If now we consider that, with a steady stimulus impinging the system, there is a wave of spikes with a defined frequency $f(I, t)$ and wavelength $\lambda(I, t)$, so that the velocity can be written as $v = \lambda f$, the previous equation becomes:

$$E = \frac{1}{2} \left(\frac{2h}{v\lambda(I, t)} \right) v^2 \quad (\text{C.5})$$

Considering now that the greatest changes in ionic currents happens at the Ranvier node (Kandel et al. 2000), we could consider as a rough approximation the changes in density in a volume $\pi r^2 d_R$, so that we have a density of energy of:

$$\epsilon(t) = \frac{1}{2} \left(\frac{2h}{\pi r^2 d_R v \lambda(I, t)} \right) v^2 \quad (\text{C.6})$$

Hence, if we consider the density of ionic currents given by:

$$\rho(t) \equiv \frac{2h}{\pi r^2 d_R v \lambda(I, t)} \quad (\text{C.7})$$

then equation (C.1) and the Hamiltonian (3.13) are equivalent. In particular, since definition (C.7) can be rewritten as:

$$\lambda(I, t) \equiv \frac{2h}{\pi r^2 d_R v \rho(t)} \quad (\text{C.8})$$

hence changes in the wavelength are related to changes in the total density of ionic currents, in particular λ increases if $\rho(t)$ decreases. Adaptation indeed occurs following the inactivation of Na^+ or Ca^{2+} channels or the activation of K^+ channels, thus reducing the density of ions inside the nerve (Kandel et al. 2000).

Appendix D

Possible derivations of (4.4)

D.1 Norwich's assumptions

A simplified model of the energy can be built on the base of two assumptions: first, internal energy decreases with time in order to account for adaptation phenomenon; second, internal energy is proportional to the probability that the sensory system discriminates a signal intensity from the background noise (or a reference signal). Given these assumptions the energy becomes:

$$E = \frac{C}{t^a} \frac{\sigma_S^2}{\sigma_S^2 + \sigma_R^2}$$

where C is a constant with the physical dimension of an action, the variable $t \in \mathcal{T}$ accounts for adaptation¹, and the ratio between the standard deviations of signal and noise accounts for the probability of discriminating signal from noise.

Following the same statistical assumptions made by Norwich (1993) the dependencies on $t \in \mathcal{T}$ and $I \in \mathbb{R}^+$ can be emphasized. In detail:

- The system draws samples of size N from the stimulus population, hence the variance σ_S^2 can be replaced by the variance of the mean σ_S^2/N .
- The sampling rate α is constant, so that $N = \alpha t$.
- The relation between the signal's standard deviation and its mean (corresponding to the stimulus intensity) follows a common statistical mechanical dependence (Jakson 1974; Huang 1987) of the order $\sigma_S^2 \propto I^n$.

The resulting energy is:

$$E = \frac{C}{t^a} \frac{\frac{\sigma_S^2}{N}}{\frac{\sigma_S^2}{N} + \sigma_R^2} \rightarrow E = \frac{C}{t^a} \frac{\beta I^n}{t + \beta I^n}$$

where β groups all the constants. The previous expression is exactly equation (4.4) for $r = 1$. Indeed, relaxing Norwich's second assumption to a non constant sampling rate gives exactly (4.4). In particular, the shape of the psychophysical law (4.13) found by Norwich (1993) corresponds to the choice $a = r = 1$.

¹In this strong approximation perception is depleted to extinction.

D.2 Fisher's Information approach

An interesting field of physics, related to the calculus of variation, derives the behavior of a system as a consequence of a variational requirement over a difference in Fisher information entropy in the system (Frieden 1988). Fisher's information can indeed be considered a measure of the precision, that is the ability in estimate a parameter, hence a difference in Fisher's information entropy measures a transition in which the knowledge about the system changes. Moving for instance from a state s_1 to a state s_2 , there is a transition in Fisher's information, that is $I_1 \rightarrow I_2$. The behavior of the system derives from the requirements that $\delta(I_2 - I_1) = 0$, that is the change in Fisher's entropy is an extremum.

Equation (4.4) can be derived from Fisher's Information Entropy. Suppose indeed that the initial state of a system is a gaussian noise, corresponding to a Fisher's information $I_N = \frac{1}{\sigma_N^2}$. Then the system is impinged by a gaussian external stimulus and moves to a state of signal plus noise, that has an information entropy $I_{S+N} = \frac{1}{\sigma_{S+N}^2}$. If the energy were related to these changes we could hypothesize:

$$E = C(I_N - I_{S+N}) = C\left(\frac{1}{\sigma_N^2} - \frac{1}{\sigma_{S+N}^2}\right)$$

that is:

$$E = C\left(\frac{1}{\sigma_N^2} \frac{\sigma_S^2}{\sigma_S^2 + \sigma_N^2}\right)$$

where C is just a proportionality constant. So, like in the previous derivation, the ratio between the standard deviations of signal and noise accounts for the probability of discriminating signal from noise. With very similar hypotheses of those of Norwich (1993):

- The system draws samples of size N from the stimulus population, hence the variance σ_S^2 can be replaced by the variance of the mean σ_S^2/N .
- The sampling rate α is not constant, so that $N = Rt^\tau$.
- The noise increases in time following a power law: $\sigma_N^2 = At^a$ and thus satisfying the I-theorem, $\frac{dI}{dt} \leq 0$ (Frieden 1988).
- The relation between the signal's standard deviation and its mean (corresponding to the stimulus intensity) follows a common statistical mechanical dependence (Jakson 1974; Huang 1987) of the order $\sigma_S^2 = \beta I^n$.

We have:

$$E = \frac{C}{At^a} \frac{\beta I^n}{ARt^{\tau+a} + \beta I^n}$$

thus taking $\tau = r - a$ gives exactly equations (4.4).

Appendix E

Dimensional analysis

The choice (4.8) has been suggested by the following dimensional analysis:

$$[R] = \frac{[I]^n}{[t]^r} \quad (\text{E.1})$$

$$[E] \approx \frac{[\Pi]^2}{[t]} \frac{[R][t]^r [I]^n}{([R][t]^r + [I]^n)^2} \approx \frac{[\Pi]^2}{[t]} \frac{[I]^{2n}}{[I]^{2n}} \approx \frac{[\Pi]^2}{[t]} \quad (\text{E.2})$$

that imply for the conjugate momentum to have the dimension of an action:

$$[\Pi]^2 = [E][t] = [A] \quad (\text{E.3})$$

then the modulating function has the dimension of a time:

$$[m] = \frac{[A]}{[E]} = [t] \quad (\text{E.4})$$

since it is a measure of the inter-spike interval.

In particular then a psychophysical continua is measured as a square root of an action:

$$[\psi] = \frac{[\Pi]}{[m]} = [A]^{\frac{1}{2}} \quad (\text{E.5})$$

Appendix F

Derivation of equation (4.5)

The general form of the psychophysical function can be derived starting from:

$$\psi(I, t) = -\frac{2}{|\Pi|} \int \mathcal{H}_P(I, t) dt$$

and using the shape of energy (4.14):

$$\mathcal{H}_P(I, t) = \frac{(\Pi)^2}{2} \frac{Rt^{r-1}(I^n - I_0^n)}{(Rt^r + I^n)(Rt^r + I_0^n)}$$

that leads to:

$$\psi(I, t) = -|\Pi| \int \frac{Rt^{r-1}(I^n - I_0^n)}{(Rt^r + I^n)(Rt^r + I_0^n)} dt$$

The integrand can be split into two parts:

$$\psi(I, t) = -|\Pi| \int \left(\frac{I^n}{t^a(Rt^r + I^n)} - \frac{I_0^n}{t^a(Rt^r + I_0^n)} \right) dt$$

that can furtherly decomposed in:

$$\psi(I, t) = -|\Pi| \int \left[\left(\frac{1}{t^a} - \frac{Rt^{r-a}}{Rt^r + I^n} \right) - \left(\frac{1}{t^a} - \frac{Rt^{r-a}}{Rt^r + I_0^n} \right) \right] dt$$

Simplifying the terms and switching signes:

$$\psi(I, t) = |\Pi| \int \left(\frac{Rt^{r-a}}{Rt^r + I^n} - \frac{Rt^{r-a}}{Rt^r + I_0^n} \right) dt$$

Collecting the dependence on a :

$$\psi(I, t) = \frac{|\Pi|}{r} \int t^{1-a} \left(\frac{Rrt^{r-1}}{Rt^r + I^n} - \frac{Rrt^{r-1}}{Rt^r + I_0^n} \right) dt$$

that can be rewritten as:

$$\psi(I, t) = \frac{|\Pi|}{r} \int t^{1-a} \left[\frac{d}{dt} \log(Rt^r + I^n) - \frac{d}{dt} \log(Rt^r + I_0^n) \right] dt$$

and then:

$$\psi(I, t) = \frac{|\Pi|}{r} \int t^{1-a} \frac{d}{dt} \log \left(\frac{Rt^r + I^n}{Rt^r + I_0^n} \right) dt$$

Integrating by parts:

$$\psi(I, t) = \frac{|\Pi|}{r} \left[t^{1-a} \log \left(\frac{Rt^r + I^n}{Rt^r + I_0^n} \right) - \int \frac{1-a}{t^a} \log \left(\frac{Rt^r + I^n}{Rt^r + I_0^n} \right) dt \right]$$

If now $a = 1$ we have psychophysical law (4.10):

$$\psi(I, t) = \frac{|\Pi|}{r} \log \left(\frac{Rt^r + I^n}{Rt^r + I_0^n} \right)$$

Whereas, if $a > 1$ or if $0 < a < 1$ the solution becomes really tangled. In our opinion this is a very interesting results since it implies that, the psychophysical law (4.10) can be obtained only when the exponent of the spike frequency adaptation is $a = 1$, that is, pure classical adaptation is the fundamental scale of the system and leads the trend of perception.

Appendix G

Derivation of Pieron's law

As it has already been stressed in section (5.1.1), in a mechanical statistical treatise the number of states that are equivalent, since they possess an energy between E and $E + \Delta E$, is measured by the entropy S that is defined as a measure of the volume occupied by the states in the phase space Γ (Huang 1987). Given then the volume of those states with Hamiltonian in between $E, E + \Delta E$:

$$\mathcal{V}(E) = \int_{E \leq H \leq E + \Delta E} d\psi d\Pi \quad (\text{G.1})$$

the entropy is defined as:

$$S(E) \equiv k \log \mathcal{V}(E) \quad (\text{G.2})$$

In particular, for the choice of Hamiltonian (3.13) it can be seen that:

$$S(I, t) = k \log \left(\frac{2R_\psi m(I, t)}{\pi} (2\Delta E)^{\frac{1}{2}} \right) \quad (\text{G.3})$$

where R_ψ is the range spanned over the psychological continuum and $m(I, t)$ is the modulating function defined in section (3.4). In particular, using now approximation (5.1) on the energy-jnds:

$$S(I, t) = k \log \left(\frac{2R_\psi (2\epsilon)^{\frac{1}{2}}}{\pi} m(I, t) \right) \quad (\text{G.4})$$

if now, for sake of simplicity we consider the limit $I_0 \rightarrow 0$ in the energy equation (4.14), we can write:

$$S(I, t) = k \log \left(C \frac{t(Rt^r + I^n)}{I^n} \right) \quad (\text{G.5})$$

where C collects all the constants. It is interesting to notice that, in the limit $I \rightarrow 0$ the energy becomes very small while the entropy increases since in the same volume there can be more states. Instead, in the limit $I \rightarrow \infty$ the entropy

decreases, so that the higher the stimulus intensity the lower the number of states in the phase space. This sounds sensible if reaction time measures the time needed to span the phase space in order to identify the stimulus: higher stimuli intensity require less time to be recognized. Furthermore, it must be noticed that entropy increases as t increases, so that psychophysical adaptation can be considered like a blurring of sensation. In particular, the minimum entropy is given in the limit $I \rightarrow \infty$:

$$\lim_{I \rightarrow \infty} S(I, t) = k \log (Ct) = S_\infty \quad (\text{G.6})$$

Now, since we are considering simple reaction times the system does not have time to adapt, so that we can take the limit $t \rightarrow 0$:

$$\begin{aligned} \lim_{t \rightarrow 0} S(I, t) &= \lim_{t \rightarrow 0} k \log \left(C \frac{t(Rt^r + I^n)}{I^n} \right) = \dots \\ \dots &= \lim_{t \rightarrow 0} k \log (Ct) + k \log \left(1 + \frac{Rt^r}{I^n} \right) \approx S_\infty + \frac{Rt^r}{I^n} \end{aligned}$$

The velocity of the span mechanism of the states must be faster than the velocity at which the entropy increases for the adaptation phenomenon, otherwise it would be impossible to resolve a state. In particular, we should expect adaptation to cease at a value τ lower than the simple reaction time t_R since the latter has to account for the travel delay of the signal along nerves and neural pathways. In particular, the entropy S_R to which the system reacts can be approximated with:

$$S_R(I, \tau) \approx S_\infty + \frac{R\tau^r}{I^n} \quad (\text{G.7})$$

where τ is then related to the maximum growth of the entropy and, at a first approximation, can be considered a constant (in such a way S_∞ is also constant).

Finally, since the reaction time should be in proportion to the space that has to be spanned, calling t_∞ the time needed to span the volume S_∞ , we have:

$$t_R : S_R(I, \tau) = t_\infty : S_\infty \quad (\text{G.8})$$

that implies:

$$t_R = t_\infty \frac{S_R(I, \tau)}{S_\infty} = t_\infty + \frac{t_\infty R \tau^r}{S_\infty I^n} \quad (\text{G.9})$$

collecting all the constants t_∞, τ, R and S_∞ gives:

$$t_R = t_\infty + \frac{C_\infty}{I^n} \quad (\text{G.10})$$

that is the Pieron Law for the simple reaction times.

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