J. Math. Biol. 52, 439–457 (2006)
Digital Object Identifier (DOI):
10.1007/s00285-005-0361-3

Mathematical Biology

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A stochastic model and a functional central limit theorem for information processing in large systems of neurons

Received: 15 March 2005 /
Published online: 28 December 2005 –

Abstract. The paper deals with information transmission in large systems of neurons. We model the membrane potential in a single neuron belonging to a cell tissue by a non time-homogeneous Cox-Ingersoll-Ross type diffusion; in terms of its time-varying expectation, this stochastic process can convey deterministic signals.

We model the spike train emitted by this neuron as a Poisson point process compensated by the occupation time of the membrane potential process beyond the excitation threshold.

In a large system of neurons $1 \leq i \leq N$ processing independently the same deterministic signal, we prove a functional central limit theorem for the pooled spike train collected from the N neurons. This pooled spike train allows to recover the deterministic signal, up to some shape transformation which is explicit.

1. Introduction

A neuron in a cell tissue receives synaptic input from a large number of other neurons. The total number of synapses contacting a single neuron is $\approx O(10^4)$; most of these are exciting synapses, contacting the dendrites of the receiving neuron, the remaining smaller part (of the order of 10 %) are inhibitory synapses, concentrating near the soma of the receiving neuron.

In a single synaptic connection, incoming spikes (action potentials generated by other neurons) cause a release of transmitter molecules at the synaptic endpoint, and create some small postsynaptic current.

A large number of synaptic connections being active at different locations and at different times, according to a complex spatio-temporal pattern, a large number of small postsynaptic currents – decayed and delayed, with varying signs and amplitudes – adds up in the soma of the receiving neuron, and decays at some rate.

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Mathematics Subject Classification (2000): 60J60, 60G55, 60F05, 62M05

Key words or phrases: Diffusion processes – Point processes – Functional central limit theorem – Parameter estimation – Stochastic neuron models – Membrane potential – Spike train – Pooled spike train – Signal – Response

This corresponds to fluctuation in time of the membrane potential in the receiving neuron. As a function of time, neurophysical recordings of the membrane potential look very much like trajectories of stochastic processes of diffusion type.

When the membrane potential exceeds some excitation threshold, the neuron is able to 'fire': in its axon, it generates spike trains (single spikes, sequences of spikes with varying interspike intervals, spike bursts, ...) which transmit information to a large number of other neurons.

In vivo, for a neuron in a cell tissue receiving information from a large number of other neurons, there is a need for stochastic modelization of both membrane potential and spike train generation. It has been observed e.g. in cortical neurons that neuronal response is higly variable, 'noisy' and irregular; in particular, identical stimuli do not lead to identical responses on repeated trials (see e.g. [M 00], [S-S-F 99], [S-N 98]). Shadlen and Newsome [S-N 98] have investigated in repeated measurements spike trains in the visual cortex of an alert monkey in response to some fixed visual stimulus (a certain moving picture): the same experiment being repeated 200 times, there is evidence for a random structure in the observed 200 spike trains. This randomness is visible in particular (see [S-N 98, Fig 1]) in the interspike intervals (ISI) over short time windows where histograms of observed ISI's fit surprisingly well to exponential distributions.

In a first part of this paper, we will view the membrane potential in the single neuron belonging to a cell tissue as a continuous stochastic processes $V = (V_t)_{t \geq 0}$, solving some stochastic differential equation. Its structure has to be compatible with two main features of a membrane potential, i.e. i) *additivity with respect to the input*, and ii) *exponential decay*. These two requirements lead naturally to a Cox-Ingersoll-Ross (CIR) type model for the membrane potential where incremental variances are proportional to the present state of the process. Assumed non time-homogeneous, the time-varying expectation of the CIR-type diffusion process plays the role of a given 'deterministic signal', thus the stochastic process of membrane potential can be understood as 'random noise conveying a deterministic signal'.

We will view the spike train generated by the single neuron belonging to a cell tissue as a random point measure. The exponential-like ISI histograms recorded by [S-N 98, Fig 1] indicate that one should think first of Poisson random measure; since the membrane potential is modelled by a stochastic process and since spikes can be emitted when the membrane potential exceeds some excitation threshold, we need a 'doubly stochastic' random measure. Hence we model the spike train generated by the single neuron as Poisson random measure compensated by the sojourn time of the membrane potential process above the excitation threshold (up to multiplication with some parameter). This provides a powerful framework for mathematical treatment of information transmission. In some aspects questionable from a biological point of view (this model for spike generation does not take into account the reduction of membrane potential after spike emission), it incorporates however interesting features of observed spike trains such as the exponential-like structure of observed ISI's in short time windows (remark 3.4).

So far, we have considered a single neuron receiving synaptic input from a large number of other neurons, and transmitting information to other neurons via a spike train.

In a second part of this paper, we consider a large number of stochastically independent neurons $i = 1, \ldots, N$ processing *the same deterministic signal*, in form of the time-varying expectation of their membrane potentials. Our main result is a functional central limit theorem (theorem 3.5) for the collection of spike trains sent out by the neurons $i = 1, \ldots, N$. Comparable to the Glivenko-Cantelli theorem in classical statistics, it shows that a weighted counting process for the pooled spike train is close – up to terms of stochastic order $O_P(N^{-1/2})$ – to a certain deterministic function, the *response*, which represents a *shape transformation* of the signal. Up to this transformation from signal to response which is explicit (remark 3.6), the pooled spike train collected from neurons $i = 1, \ldots, N$ *allows to recover the deterministic signal* asymptotically as $N \to \infty$. Also *subthreshold* signals can be transmitted in this way.

There are error terms of stochastic order $O_P(N^{-1/2})$ between the observed quantity – the weighted counting process for the pooled spike train from N neurons – and the response. We have a limiting Gaussian process for these. Two independent sources of error appear in the limit: first a Brownian motion time-changed by the response function, and second some Gaussian process whose covariance kernel measures dependency in the CIR type process of membrane potential.

The paper is organized as follows: in section 2, we present the CIR-type model for the membrane potential in the single neuron (from [B-H 04]). In section 3.1, we formulate a simple 'doubly stochastic' Poisson model for the spike train emitted by one neuron. Section 3.2 contains the main result (theorem 3.5) on signal transmission in large systems of neurons; this theorem is proved in section 5. Finally, section 4 proposes some methods for model check and parameter estimation.

2. A stochastic model for the membrane potential

We discuss a time-inhomogenous diffusion process of Cox-Ingersoll-Ross (CIR) type modelling two important properties of membrane potentials: i) additivity in the input, and ii) exponential decay. In subsection 2.1, we recall the classical CIR diffusion (no biologically relevant scaling, time-constant input only), see [C-I-R 85], [I-W 89, p. 235], and e.g. [O-R 97], [O 98]. Biologically relevant scaling and the effects of time-varying input will be the topic of subsection 2.2.

In neuronal models, CIR diffusions appear already in [L-L 87, (4.12) and Thm. 4], [G-L-N-R 88, (3.10), (3.27), Sect. 4], [L-S-T 95, (18)]; initially, the feature of restricted state space seemed to be of main interest. With unbounded state space, Ornstein-Uhlenbeck (OU) models have been widely used for the membrane potential, see [D-L 05], [L-S 01], [S-S-F 99], [L-S 99], [L-L 87] and the literature quoted there. OU models map well the property ii) (exponential decay) of membrane potentials, but are questionable with respect to property i) (additivity in the input): synaptic input from a large number of stochastically active sources should imply that incremental variances of the membrane potential are proportional to the present state. CIR diffusions realize both requirements i) and ii).

2.1. Preliminaries

Consider some time constant $\tau > 0$, and parameters $a > 0$, $\sigma^2 > 0$ such that

$$\frac{2a}{\sigma^2} > 1. \tag{1}$$

For constants $f \geq 0$ representing some time-constant level of 'input', we write $\xi = \xi^f$ for the real-valued stochastic process $(\xi_t^f)_t$ solution to the stochastic differential equation (SDE)

$$d\xi_t^f = \left[a + f - \xi_t^f\right](\tau dt) + \sigma\left[\xi_t^f \vee 0\right]^{\frac{1}{2}}\left(\tau^{\frac{1}{2}} dW_t\right) \tag{2}$$

on some time interval $[0, T]$, with driving standard Brownian motion W. We prescribe some deterministic starting point $\xi_0^f > 0$, or some initial law concentrated on $(0, \infty)$. Up to the somewhat unusual parametrization, (2) is the well known CIR (or mean reverting) diffusion. See [M 82] and [K-S 91] for background on stochastic processes and SDE's.

We recall known properties of this process. Under (1), trajectories of ξ^f are continuous functions $[0, T] \to (0, \infty)$ (cf. [I-W 89, p. 235–237]), and we suppress truncation by 0 in the diffusion coefficient of (2). Viewed on the time interval $[0, \infty)$, the process $(\xi_t^f)_{t \geq 0}$ is ergodic; the invariant law is the Gamma distribution

$$\Gamma\left(\frac{2}{\sigma^2}(a + f), \frac{2}{\sigma^2}\right) \quad \text{on} \quad (0, \infty) \tag{3}$$

(see e.g. the first pages of [K 03]). Mean and variance of (3)

$$(a + f), \quad \frac{\sigma^2}{2}(a + f)$$

are linear in the input f. We think of the case $f = 0$ (no input) as remaining randomness in a system at rest. For constant $f \geq 0$, we will always consider the CIR diffusion $(\xi_t^f)_t$ in (2) as a stationary process, taking as initial condition the invariant law (3).

Note that the invariant law (3) is free of the time constant τ. Large values of τ correspond to rapid oscillations in the trajectory of $(\xi_t^f)_t$. As a rate of decay, τ represents a backdriving force reorienting trajectories towards $(a + f)$. Note that a time constant τ for the process ξ – solving a Wiener driven SDE – must affect both dt and the angle brackett $d\langle M^\xi\rangle_t$ of the martingale part M^ξ of ξ. The inverse of τ is the membrane time constant in the biological sense.

2.2. Time-inhomogeneous CIR diffusion as a model for the membrane potential

Commonly, the potential difference at the membrane K_R in a neuron 'at rest' is put to -70 mv, and the excitation threshold K_E to -50 mv. In fact, there exists a

broad variety of values according to different types of neurons and different experimental conditions (e.g., levels of pharmaka administrated to a cell tissue under observation). Hence we start from constants

$$K_R < K_E$$

for a resting level and an excitation threshold.

Consider first the case $f \equiv 0$ (no input) in SDE (2). A neuron belonging to a cell tissue will always remain exposed to some network activity 'at rest'. We introduce a linear scaling

$$S(y) = s_0 + s_1 y, \quad s_0 \in I\!R, \quad s_1 > 0 \tag{4}$$

with coefficients such that the stationary process $\left(S\left(\xi_t^0\right)\right)_t$ with $f \equiv 0$ is a reasonable model for the membrane potential in a neuron 'at rest', i.e.

i) some left endpoint s_0 for the support of $\mathcal{L}\left(S\left(\xi_t^0\right)\right)$ is specified;

ii) the constant K_R is understood as expected value of $\mathcal{L}\left(S\left(\xi_t^0\right)\right)$:

$$E\left(S\left(\xi_t^0\right)\right) = s_0 + s_1 a \quad \stackrel{!}{=} K_R; \tag{5}$$

iii) the variance is adapted to realistic fluctuations of a membrane potential 'at rest':

$$Var\left(S\left(\xi_t^0\right)\right) = s_1^2 \frac{\sigma^2}{2} a \quad \stackrel{!}{=} \quad \text{some empirically assessed quantity.} \tag{6}$$

As an example, having observed a (stationary process of) membrane potential 'at rest' over a long time interval, almost continuously in time (i.e. on some fine grid of time points), we dispose of an occupation time measure whose support, mean and variance correspond to i)–iii).

We turn to time-varying input f in SDE (2). Consider a function $f : [0, T] \to [0, \infty)$, right-continuous and piecewise Lipschitz. This allows e.g. for input of type 'on/off' like

$$f(t) := c \text{ if } t_{\text{on}} \le t < t_{\text{off}},\ f(t) := 0 \text{ else},$$
$$f(t) := c \cdot \sin\left(\pi \frac{t - t_{\text{on}}}{t_{\text{off}} - t_{\text{on}}}\right) \text{ if } t_{\text{on}} \le t \le t_{\text{off}},\ f(t) := 0 \text{ else}.$$

The following has been proposed in [B-H 04] as a model for the membrane potential in a neuron belonging to a cell tissue under time-varying input.

Definition 2.1. For $f : [0, T] \to [0, \infty)$ right-continuous and piecewise Lipschitz, the *CIR model for the membrane potential under input* f is the stochastic process

$$V^f = \left(V_t^f\right)_{t \in [0,T]}, \quad V_t^f := S\left(\xi_t^f\right) \tag{7}$$

with $S(\cdot)$ of (4), where $\left(\xi_t^f\right)_t$ is solution to the SDE with time-varying coefficients

$$d\xi_t^f = \left[a + f(t) - \xi_t^f\right](\tau dt) + \sigma\left[\xi_t^f\right]^{\frac{1}{2}}\left(\tau^{\frac{1}{2}} dW_t\right) \quad \text{on } [0,T] \tag{8}$$

with initial law

$$\mathcal{L}\left(\xi_0^f\right) = \Gamma\left(\frac{2}{\sigma^2}(a + f(0)), \frac{2}{\sigma^2}\right).$$

The processes $\left(V_t^f\right)_{0\le t\le T}$ are strongly Markov, time-inhomogeneous, and (s_0,∞)-valued. Up to now, by (7) + (8), the membrane potential at rest V^0 is parametrized by $s_0, s_1 a, s_1\frac{\sigma^2}{2}, \tau$, and time-varying input $f(\cdot)$ appears in the SDE for V^f in the form $s_1 f(\cdot)$. There are no intrinsic norming constants for the input functions, hence we may *reparametrize and put*

$$s_1 := 1 \tag{9}$$

in all equations of this subsection, and in the sequel: then $S(\cdot)$ in (4)–(6) is a shift, V^f solves

$$\begin{aligned} dV_t^f = &\left[K_R + f(t) - V_t^f\right](\tau dt) \\ &+\sigma\left[V_t^f - s_0\right]^{\frac{1}{2}}\left(\tau^{\frac{1}{2}} dW_t\right) \quad \text{on } [0,T], \end{aligned} \tag{10}$$

and the law of the process $\left(V_t^f\right)_{0\le t\le T}$ is uniquely determined from

$$s_0, a, \frac{\sigma^2}{2}, \tau \quad \text{and} \quad f(\cdot). \tag{11}$$

Remark 2.2. We speak of a *fast diffusion* V^f if the time constant τ is large compared to $1 + L$, L some Lipschitz constant for $f(\cdot)$ on its continuity intervals. In fast diffusions, we observe locally at continuity points of f a close-to-stationary behaviour of the process V^f, in the sense of good approximations

$$E\left(V_t^f\right) \approx S(a + f(t)) = K_R + f(t), \quad Var\left(V_t^f\right) \approx \frac{\sigma^2}{2}(a + f(t)),$$
$$P\left(V_t^f \in A\right) \approx \Gamma\left(\frac{2}{\sigma^2}(a + f(t)), \frac{2}{\sigma^2}\right)(A - s_0), \quad A \in \mathcal{B}(\mathbb{R}),$$

at continuity points t of $f(\cdot)$. Simulated trajectories of V^f will allow to judge the accuracy of such approximations; an illustration is in [B-H 04, Fig. 2–3].

Definition 2.3. We call the function

$$I_1^f : [0,T] \ni t \longrightarrow E\left(V_t^f\right) \in [K_R, \infty)$$

signal contained in the membrane potential $\left(V_t^f\right)_{0\le t\le T}$. A signal I_1^f is called *subthreshold* if

$$\sup_{0\le t\le T} E\left(V_t^f\right) < K_E,$$

with K_E the excitation threshold as in the beginning of this subsection.

A subthreshold signal corresponds to some input f not strong enough to lift the expected value of the membrane potential beyond the excitation threshold. The membrane potential itself – as a stochastic process V^f according to (7)–(8) – will always spend with positive probability some amount of time beyond the excitation threshold. Even the system at rest – case $f(\cdot) \equiv 0$ – will produce from time to time (perhaps extremely rarely) some spikes. This is the reason why stochastic neuron models – in contrast to deterministic models – are able to explain information transmission in large systems of neurons, even for signals which are subthreshold.

3. Spike generation and information transmission: a Poisson model

The spike trains recorded by [S-N 98, Fig. 1] in the visual cortex – repeated measurements of spike trains in response to the same stimulus, evaluated in small time windows where a spike density per time unit seems locally homogeneous – yield histograms of interspike intervals (ISI) which are close to an exponential distribution. This motivates to study a simple Poisson model for spike generation. This model is certainly questionable from a biological point of view (for example, it does not take into account the reduction of membrane potential after spike emission, see [G-L-N-R 88], [L-S-T 95], or e.g. [T 89, Ch. 5.3.2] [S-S-F 99, section 4], [D-L 05] in OU-framework). However, it provides a framework for mathematical study of information transmission in large systems of neurons.

3.1. The single neuron: a simple Poisson model for spike generation

We consider a single neuron belonging to a cell tissue, and take its membrane potential as a CIR type diffusion $\left(V_t^f\right)_{t\in[0,T]}$ as in (7)–(11), for some fixed input function $f : [0, T] \to [0, \infty)$. A spike train generated by the neuron in the time interval $[0, T]$ is a random sequence

$$0 < T_1 < \cdots < T_M \le T$$

of time points in $[0, T]$, of random length $M \in \mathbb{N}_0$, written equivalently as a random measure

$$\mu(dy) := \sum_{j=1}^{M} \epsilon_{(T_j)}(dy) \quad \text{on} \quad ([0, T], \mathcal{B}([0, T])) . \tag{12}$$

Definition 3.1. μ in (12) is called a *Poisson spike train* if

μ is Poisson random measure (PRM) with intensity $\lambda \cdot 1_{\{V^f \geq K_E\}}(s)ds$ on $[0, T]$

with K_E the excitation threshold, for some parameter $\lambda > 0$.

In a Poisson spike train, spikes are generated at the jump times of a Poisson process whose compensator is (up to multiplication with the parameter $\lambda > 0$) the occupation time of the membrane potential V^f beyond the excitation threshold.

Definition 3.2. We call the function

$$I_2^f : [0, T] \ni t \longrightarrow P\left(V_t^f \geq K_E\right) \in (0, 1)$$

response of a neuron with membrane potential V^f.

Remark 3.3. In fast diffusions and at continuity points t of $f(\cdot)$, the value $I_2^f(t)$ of the response is close to the proportion of time per time unit which a trajectory of V^f is expected to spend beyond the excitation threshold near time t; we have an approximation by remark 2.2

$$I_2^f(t) \approx \Gamma\left(\frac{2}{\sigma^2}(a + f(t)), \frac{2}{\sigma^2}\right)([K_E - s_0, \infty)).$$

Remark 3.4. In Poisson spike trains emitted by a single neuron, interspike intervals (ISI) generated conditionally on a 'fast' or on a 'slow' diffusion V^f will exhibit a remarkable difference. We think of a signal I_1^f which remains subthreshold or at the threshold.

a) *Slow diffusions*: a substantial amount of excursions of V^f beyond the excitation threshold will be 'long' excursions during which several spikes can be emitted. The corresponding ISI's are exponentially distributed with parameter λ. In contrast to these, ISI's intersecting different excursions of V^f tend to be essentially longer. In repeated measurements from the same neuron, with same input f and independent realizations of the pair (μ, V^f), ISI's recorded in some fixed time window (as in [S-N 98, fig. 1]) will correspond statistically to a mixture model which delivers with some probability $0 < q < 1$ exponentially-λ-distributed waiting times, and with probability $1 - q$ waiting times of a different structure. Among ISI's observed in a short time window, the first ones tend to be predominant.
b) *Fast diffusions*: excursions of the membrane potential V^f above the excitation threshold will be extremely short and will alternate rapidly with visits below. In this case, by definition of I_2^f and by 3.3, the empirical distribution function of ISI's collected near t will be close to an exponential law with parameter $\lambda \cdot I_2^f(t)$.

3.2. Signal processing by a large number of neurons: a functional central limit theorem for pooled Poisson spike trains

Consider stochastically independent neurons i processing the same input f. Write $V^{i,f}$ for the membrane potential in neuron i, and μ^i for the spike train emitted by neuron i. With fixed values of the parameters which are common to all neurons under consideration, we thus have iid pairs

$$\left(V^{f,i}, \mu^i\right), \quad i \geq 1$$

defined on some $(\Omega, \mathcal{A}, P)$. We introduce a weighted counting process

$$\Psi_N(t,\omega) := \frac{1}{N}\sum_{i=1}^{N} \mu^i(\omega, [0,t]), \quad \omega \in \Omega, 0 \leq t \leq T$$

for the *pooled spike train* collected from neurons $1 \leq i \leq N$, and introduce processes

$$A^{i,f}(t,\omega) := \int_0^t 1_{[K_E,\infty)}\left(V_s^{i,f}(\omega)\right) ds, \quad 1 \leq i \leq N$$

$$\Phi_N(t,\omega) := \frac{1}{N}\sum_{i=1}^{N} A^{i,f}(t,\omega)$$

$$\Phi^f(t) := E\left(A_t^{1,f}\right) = \int_0^t I_2^f(s)ds.$$

With $\lambda\!\!\!^{-}$ the Lebesgue measure, we will work on the (Polish) path space

$$\mathbb{L} := L^2([0,T], \mathcal{B}([0,T]), \lambda\!\!\!^{-}) \quad \text{with Borel } \sigma\text{-field denoted by } \mathcal{B}(\mathbb{L})$$

of measurable functions $h : [0,T] \to \mathbb{R}$ with $\|h\| := \left(\int_0^T |h|^2(t)dt\right)^{1/2} < \infty$. All processes above are measurable in (t,ω), and their paths are bounded functions $[0,T] \to \mathbb{R}$. This implies that $\omega \to \Psi_N(\cdot,\omega)$, $\omega \to \Phi_N(\cdot,\omega)$ etc. are random variables on $(\Omega, \mathcal{A})$ taking values in $(\mathbb{L}, \mathcal{B}(\mathbb{L}))$.

The following – a Glivenko-Cantelli type theorem for weighted counting processes of pooled spike trains – is the main result of this paper.

Theorem 3.5. We have

$$\sqrt{N}\left(\Psi_N - \lambda\Phi^f\right) \longrightarrow W \quad \text{(weak convergence in } \mathbb{L}, \text{ as } N \to \infty)$$

where $W = (W_t)_{t\in[0,T]}$ is a Gaussian process with covariance kernel

$$K(t_1,t_2) := \lambda \cdot \Phi^f_{t_1\wedge t_2} + \lambda^2 \cdot \int_0^{t_1}\int_0^{t_2} dr_1 dr_2 \check{K}^f(r_1,r_2),$$

$$\check{K}^f(r_1,r_2) := P\left(V_{r_i}^f \geq K_E, i = 1,2\right) - \prod_{i=1}^{2} P\left(V_{r_i}^f \geq K_E\right).$$

The proof of theorem 3.5 will be given in section 5.

The covariance kernel of W in 3.5 is a sum of two terms. The first one is the covariance kernel of $\sqrt{\lambda} \cdot B$ time-changed by $t \to \Phi^f(t)$, where B is standard Brownian motion. Standing alone, this would be the limiting process if instead of the pooled spike train from N neurons, N independent Poisson processes with *deterministic intensity* $\lambda \cdot I_2^f(\cdot)$ were observed (see e.g. [K 98]).

The second term in the covariance kernel is due to the 'doubly stochastic' character of the model in subsection 3.1. It integrates $\check{K}^f(\cdot,\cdot)$ as a measure of dependency between variables $V_{r_i}^f$, $r_1, r_2 \in [0, T]$. In the limit of fast diffusions, this second contribution will disappear.

Remark 3.6. a) As a consequence of theorem 3.5, large systems of stochastically independent neurons – processing the same time-dependent input f via a pair $(\mu^i, V^{f,i})$ – are able to transmit (subthreshold) signals. In this transmission, the signal undergoes some structural deformation of its shape, described by the passage from the function I_1^f to the function $\lambda \cdot I_2^f$. The pooled spike train from neurons $1 \le i \le N$ allows to recover I_2^f in integrated form, multiplied by λ, up to error terms of stochastic order $1/\sqrt{N}$.

b) Comparing 3.5 and 3.4 a), a remarkable consequence arises. In case of slow diffusions V^f – which seems to be the more relevant case for biological observations – *interspike times* obtained from repeated measurements *in a single neuron* in restriction to some small time window (data sets as in [S-N 98, fig. 1] or as in [S-S-F 99, fig. 2]) will not allow to recover the function I_2^f in this time window, hence *will not allow to recover the signal* I_1^f. This is possible only through the *pooled spike train from a large number of neurons*, in virtue of 3.5.

4. Methods for model check

This is a discussion section devoted to methods for model check and parameter estimation related to subsections 2.2 and 3.1. Suppose we observe a neuron which in successive experiments is exposed artificially (e.g. by administration of suitable pharmaka or by injection of current) to different regimes of time-constant input such that the main characteristics of the cell, in particular the value of its excitation threshold, remain unaffected.

Measuring in K different regimes the membrane potential at n discrete time points with small step size Δ, we dispose of a data set

$$X_0^k, X_\Delta^k, X_{2\Delta}^k, \ldots, X_{n\Delta}^k, \quad 1 \le k \le K. \tag{13}$$

For $1 \le k \le K$, introduce empirical means and variances

$$m_n^k := \frac{1}{n} \sum_{i=1}^n X_{i\Delta}^k, \quad d_n^k := \frac{1}{n} \sum_{i=1}^n \left(X_{i\Delta}^k - m_n^k \right)^2,$$

occupation measures (with notation ϵ_a for Dirac measure sitting in a)

$$\frac{1}{n} \sum_{i=1}^n \epsilon_{(X_{i\Delta}^k)} \tag{14}$$

and relative frequencies for visits beyond the excitation threshold

$$e_n^k := \frac{1}{n}\sum_{i=1}^{n} 1_{[K_E,\infty)}(X_{i\Delta}^k).$$

If the model of subsection 2.2 for the membrane potential is appropriate, the following holds:

Model hypothesis (H): For every k, the data set $X_0^k, X_\Delta^k, \ldots, X_{n\Delta}^k$ stems from a stationary process $\left(V_t^f\right)_t$ observed at times $t = \Delta, 2\Delta, \ldots, n\Delta$ where $n\Delta = T$, for some value of a time-constant input $f(\cdot) \equiv f \geq 0$ which varies with k. The parameters s_0, a, $\frac{\sigma^2}{2}$, τ in (11) as well as the value K_E of the excitation threshold do not change with k.

Under *(H)*, by stationarity of V^f, the following quantites do not depend on $0 \leq t \leq T$:

$$E\left(V_t^f\right) \equiv s_0 + (a+f) = K_R + f, \quad Var\left(V_t^f\right) \equiv \frac{\sigma^2}{2}(a+f), \tag{15}$$

$$P\left(V_t^f \in A\right) \equiv \Gamma\left(\frac{2}{\sigma^2}(a+f), \frac{2}{\sigma^2}\right)(A - s_0), \quad A \in \mathcal{B}(\mathbb{R}), \tag{16}$$

$$\left(E\left(V_t^f\right), P\left(V_t^f \geq K_E\right)\right) \equiv: (i_1^f, i_2^f) \tag{17}$$

which is the pair signal-response of 2.3 and 3.2 for time-constant input f. In the simple setting of *(H)*, we can sharpen remark 3.6: there is a *transfer function* $T : [K_R, K_E] \to (0,1)$, smooth and strictly increasing, with the property $T(i_1^f) = i_2^f$ for arbitrary constant $f \geq 0$; it is given by

$$T(x) = \Gamma\left(\frac{2}{\sigma^2}(x - s_0), \frac{2}{\sigma^2}\right)([K_E - s_0, \infty)), \quad K_R \leq x \leq K_E. \tag{18}$$

Of course, for n sufficiently large, all occupation measures (14) taken separately should be close to suitably shifted Gamma densities. The following allows to validate (or to invalidate) the model of subsection 2.2 for the membrane potential in the subthreshold domain.

4.1. Model check

Under *(H)*, for Δ small and n large,

a) a plot of empirical variances against empirical means in the data set (13)

$$\left(m_n^k, d_n^k\right), \quad 1 \leq k \leq K \tag{19}$$

should present a convincing close-to-linear structure, cf. (15);

b) by linear regression in (19) – explaining the empirical variances by the empirical means – we estimate $\frac{\sigma^2}{2}$ by the slope of the regression line $\widehat{\ell}_n$, and s_0 by the zero of $\widehat{\ell}_n$;

c) we estimate the time constant τ by the solution of

$$\frac{1}{2}\sum_{k=1}^{K}\sum_{i=1}^{n}\left[X_{i\Delta}^{k}-X_{(i-1)\Delta}^{k}\right]^2 \stackrel{!}{=} \tau\frac{\sigma^2}{2}T\sum_{k=1}^{K}\left[m_n^k-s_0\right] \tag{20}$$

with estimated values from b) plugged in for s_0 and $\frac{\sigma^2}{2}$ (note that the inverse $\frac{1}{\tau}$ should represent a biologically plausible value for a membrane time constant);

d) a plot of relative frequencies of visits beyond K_E against empirical means in the data set (13)

$$\left(m_n^k, e_n^k\right), \quad 1 \le k \le K$$

should be close to the graph of the transfer function, with estimated values from b) replacing the parameters s_0 and $\frac{\sigma^2}{2}$ in (18);

e) from a given value of $K_R = s_0 + a$, we estimate by b) all three parameters $s_0, a, \frac{\sigma^2}{2}$ determining the stationary law of the membrane potential at rest.

Sketch of proof. Assertions a) and c) require some comments.

a) For constant f, the discrete-time processes $\left(V_{i\Delta}^{f}\right)_{i=0,1,\ldots}$ are ergodic with invariant law given by (16). By the strong law of large numbers for ergodic Markov chains, the quantities $\frac{1}{n'}\sum_{i=1}^{n'} V_{i\Delta}^{f}$ and $\frac{1}{n'}\sum_{i=1}^{n'}\left(V_{i\Delta}^{f}\right)^2$ converge a.s. as $n' \to \infty$ to the first and second moment of $\mathcal{L}(V_t^f)$, independent of t by the stationarity assumption.

With notation $\ell(x) = \frac{\sigma^2}{2}(x - s_0)$ we have $Var(V_t^f) = \ell\left(E(V_t^f)\right)$ in (15), for arbitrary values of constant $f \ge 0$. Hence under *(H)*, for every fixed value of Δ and for $1 \le k \le K$, we will have good approximations $d_n^k \approx \ell\left(m_n^k\right)$ for the empirical quantites when n is large.

c) i) Under *(H)* and continuous-time observation, the quadratic variation process $\left[\xi^f\right]$ of the semimartingale ξ^f solving (2) is compensated by the predictable quadratic variation $\langle\xi^f\rangle$

$$\langle\xi^f\rangle_t = \tau\sigma^2\int_0^t \xi_s^f\,ds, \quad t \in [0,T].$$

In terms of V^f, this reads

$$\frac{1}{2}\langle V^f\rangle_t = \tau\frac{\sigma^2}{2}\int_0^t\left[V_s^f - s_0\right]ds, \quad t \in [0,T].$$

For Δ tending to 0 and n tending to ∞ such that $T = \Delta n$ remains fixed, the quadratic variation $\left[V^f\right]$ can be approximated by a sum of quadratic increments, and the last integral by a discrete sum; hence we solve an approximate martingale estimating equation

$$\frac{1}{2}\sum_{i=1}^{n}\left[X_{i\Delta}^{k}-X_{(i-1)\Delta}^{k}\right]^2 \stackrel{!}{=} \tau\frac{\sigma^2}{2}T\left[\frac{1}{n}\sum_{i=1}^{n}X_{(i-1)\Delta}^{k}-s_0\right] \tag{21}$$

with estimated values - from b) - plugged in for s_0 and $\frac{\sigma^2}{2}$.

ii) Up to now, we have used any one of the data sets $\left(X^k_{i\Delta}\right)_{i=0,\ldots,n}$. (20) is obtained in the same way as (21), working for $1 \le k \le K$ on all data sets simultaneously. □

In 4.1, we never need explicit values for the constants $f \ge 0$ in equation (2); it is sufficient to have data under different regimes f. Any specification of a value corresponding to a particular regime and its biophysical background may remain unknown as long as *(H)* holds.

The following allows to check the Poisson spike train model considered in subsection 3.1.

4.2. Model check

Assume *(H)* validated for the membrane potential. In addition to data (13), suppose we have counted in every measurement $1 \le k \le K$ the total number M^k_T of spikes emitted by the neuron over the time interval $[0, T]$.

Under *(H)*, for fixed Δ and n large (hence also $T = n\Delta$ large), the set of points

$$\left(m^k_n, M^k_T/T\right)_{1\le k\le K} \tag{22}$$

should allow for a convincing fit with respect to the one-parameter family

$$\left(m^k_n, \lambda \cdot e^k_n\right)_{1\le k\le K} : \lambda > 0; \tag{23}$$

we estimate λ through a best approximation (least squares, or some minimum distance approach).

Sketch of proof. Using the model for spike generation in subsection 3.1 with constant f on $[0, \infty)$, the strong law of large numbers for $(V_t^f)_{t\ge 0}$ gives with notation of (17)

$$\frac{1}{t}A^f(t) \longrightarrow \lambda \cdot i^f_2 \quad \text{a.s. as } t \to \infty.$$

In measurement $1 \le k \le K$, write $M^k(r)$ for the total number of spikes counted up to time r. The martingale convergence theorem applied to the sequence of martingales

$$\left(\frac{1}{\sqrt{t}}\left(M^k(st) - \lambda A^f(st)\right)\right)_{s\ge 0}, \quad t \to \infty$$

(with f associated to k) shows weak convergence in $\mathbb{D}$ as $t \to \infty$ to

$$\sqrt{\lambda i^f_2} \cdot B$$

with standard Brownian motion B. Hence for large t, $\frac{1}{t}M^k(t)$ will be close to $\frac{1}{t}A^f(t)$ – and thus close to λi^f_2 – up to terms of stochastic order $1/\sqrt{t}$. It remains to replace i^f_2 by the empirical quantity e^k_n discussed in 4.1 d). □

5. Proof of theorem 3.5

Write $E = \mathbb{R}^d$, for some $d \geq 1$, and $\mathbb{L}_E = L^2_E([0,T], \mathcal{B}([0,T]), \lambda\!\!\!^{-})$ for the space of all measurable functions $h : [0,T] \to E$ such that $\|h\| = \left(\int_0^T |h|^2(s)ds\right)^{1/2}$ is finite. Let $X^n, n \geq 1, X$ be E-valued processes on $(\Omega, \mathcal{A}, P)$, measurable in (t,ω), with paths in $\mathbb{L}_E$. Then

$$X^n \longrightarrow X \quad \text{(weak convergence in } \mathbb{L}_E, \text{ as } n \to \infty) \tag{24}$$

is implied (see [C-K 86, theorem 2 and remark], or [G 76, theorem 3] in case $E = \mathbb{R}$) by the following two conditions i) and ii):

i) there is a Borel set $N \subset [0,T]$ of Lebesgue measure 0 such that

$$\mathcal{L}\left((X^n_{t_1}, \ldots, X^n_{t_l}) \mid P\right) \longrightarrow \mathcal{L}\left((X_{t_1}, \ldots, X_{t_l}) \mid P\right)$$
$$\text{(weak convergence in } E^l, \text{ as } n \to \infty)$$

for all $l \geq 1$ and arbitrary $t_1, t_2, \ldots, t_l$ in $[0,T]\backslash N$;

ii) there is some function $f \in L^1_{\mathbb{R}}([0,T], \mathcal{B}([0,T]), \lambda\!\!\!^{-})$ such that for $t \in [0,T]\backslash N$

$$\sup_{n\geq 1} E\left(\left|X^n_t\right|^2\right) \leq f(t) \quad \text{and} \quad \lim_{n\to\infty} E\left(\left|X^n_t\right|^2\right) = E\left(|X_t|^2\right).$$

The proof of theorem 3.5 – via some auxiliary results – will be completed in 5.3; all notations and assumptions are as subsection 3.2.

Proposition 5.1. We have

$$\sqrt{N}\left(\Phi_N - \Phi^f\right) \longrightarrow \widetilde{W} \quad \text{(weak convergence in } \mathbb{L}_{\mathbb{R}}, \text{ as } N \to \infty)$$

where $\widetilde{W} = (\widetilde{W}_t)_{t\in[0,T]}$ is a Gaussian process with covariance kernel

$$\widetilde{K}(t_1,t_2) = \int_0^{t_1}\int_0^{t_2} dr_1 dr_2 \check{K}^f(r_1,r_2), \quad t_1, t_2 \in [0,T].$$

Proof. 1) Since $(t_1,t_2) \to \widetilde{K}(t_1,t_2)$ is symmetric and continuous on $[0,T]\times[0,T]$, a real-valued (centred) Gaussian process $\widetilde{W} = (\widetilde{W}_t)_{t\in[0,T]}$ with covariance kernel $\widetilde{K}(\cdot,\cdot)$ exists (see [L 63, p. 478], [G-S 74, chapter IV.3], [Z 75]).

2) We prove convergence as $N \to \infty$ of finite-dimensional distributions of

$$\widetilde{W}^N := \sqrt{N}\left(\Phi_N - \Phi^f\right) = \frac{1}{\sqrt{N}}\sum_{i=1}^N \left(A^{i,f} - \Phi^f\right)$$

to those of $\widetilde{W}$. Consider arbitrary $l \geq 1$, $t_1, \ldots, t_l$ in $[0,T]$; write $\Sigma := \left(\widetilde{K}(t_r, t_{r'})\right)_{1\leq r,r'\leq l}$. Using Cramér-Wold, we have to prove for all $\alpha = (\alpha_1, \ldots, \alpha_l) \in \mathbb{R}^l$:

$$\mathcal{L}\left(\sum_{r=1}^l \alpha_r \widetilde{W}^N_{t_r}\right) \longrightarrow \mathcal{N}\left(0, \alpha^\top \Sigma \alpha\right) = \mathcal{L}\left(\sum_{r=1}^l \alpha_r \widetilde{W}_{t_r}\right), \quad N \to \infty. \tag{25}$$

Define

$$R_i := \int_0^T ds \left(\sum_{i=1}^{l} \alpha_r 1_{[0,t_r]}(s) \right) \left(1_{[K_E,\infty)}(V_s^{f,i}) - P(V_s^f \geq K_E) \right), \quad i \geq 1.$$

Then R_i, $i \geq 1$, are iid, bounded and centred, so the classical central limit theorem shows

$$\sum_{r=1}^{l} \alpha_r \widetilde{W}_{t_r}^N = \frac{1}{\sqrt{N}} \sum_{i=1}^{N} R_i \longrightarrow \mathcal{N}(0, Var(R_1)) \quad \text{(weakly in } I\!R, \text{ as } N \to \infty)$$

where

$$\begin{aligned} Var(R_1) &= \int_0^T \int_0^T ds ds' \left(\sum_{r=1}^{l} \alpha_r 1_{[0,t_r]} \right)(s) \check{K}^f(s,s') \left(\sum_{r'=1}^{l} \alpha_{r'} 1_{[0,t_{r'}]} \right)(s') \\ &= \sum_{r,r'=1}^{l} \alpha_r \widetilde{K}(t_r, t_{r'}) \alpha_{r'} = \alpha^\top \Sigma \alpha. \end{aligned}$$

Hence (25) is proved, and convergence of finite dimensional distributions follows.

3) The function $f(t) := \widetilde{K}(t,t)$ is bounded on $[0,T]$. As a particular case of the calculation of $Var(R_1)$ in step 2), we have

$$E\left(\left(\widetilde{W}_t \right)^2 \right) = \widetilde{K}(t,t) = E\left(\left(\widetilde{W}_t^N \right)^2 \right) \quad \text{for all } N. \tag{26}$$

With (25) and (26), all conditions of [C-K 86, theorem 2] or [G 76, theorem 3] are satisfied, and proposition 5.1 is proved. □

Proposition 5.2. We have

$$\sqrt{N}\,(\Psi_N - \lambda \Phi_N) \longrightarrow \sqrt{\lambda} \cdot B \circ \Phi^f =: \widetilde{\widetilde{W}} \quad \text{(weak convergence in } I\!L_{I\!R}, \text{ as } N \to \infty)$$

where $B = (B_t)_{t \geq 0}$ is a standard Brownian motion independent of the limit process $\widetilde{W}$ appearing in 5.1, and where $B \circ \Phi^f$ denotes B time-changed by the deterministic function $t \to \Phi^f(t)$.

Proof. 1) Note that $t \to \Phi^f(t)$ is continuous and stricly increasing on $[0,T]$. The covariance kernel of $\widetilde{\widetilde{W}} = (\widetilde{\widetilde{W}}_t)_{t \in [0,T]}$ is

$$\widetilde{\widetilde{K}}(t_1, t_2) = \lambda \Phi^f(t_1 \wedge t_2), \quad t_1, t_2 \in [0,T].$$

2) Prepare a new probability space $(\Omega_1, \mathcal{A}_1, P_1)$ supporting a Poisson random measure $\widehat{\mu}$ with constant intensity λ on $[0,\infty)$. Consider processes

$$B_N(t) := \frac{1}{\sqrt{N}} \left(\widehat{\mu}\left([0, t \cdot N]\right) - \lambda \cdot t \cdot N \right), \quad t \geq 0$$

on $(\Omega_1, \mathcal{A}_1, P_1)$, and filtrations

$$\widehat{I\!F}^N = \left(\widehat{\mathcal{F}}_t^N\right)_{t\geq 0}, \quad \widehat{\mathcal{F}}_t^N := \sigma\left(B_N(s) : 0 \leq s \leq t\right)$$
$$= \sigma\left(\widehat{\mu}([0,s]) : 0 \leq s \leq t \cdot N\right)$$

in $\mathcal{A}_1$, for $N \geq 1$. For every N, B_N is an $\widehat{I\!F}^N$-martingale with deterministic angle brackett

$$\langle B_N \rangle_t = \lambda \cdot t, \quad t \geq 0 \tag{27}$$

and with jumps bounded by $\frac{1}{\sqrt{N}}$. It is well known that by the martingale convergence theorem (Jacod and Shiryaev [J-Sh 87, VIII.3.11])

$$B_N \longrightarrow \sqrt{\lambda} \cdot B \quad \text{(weak convergence in } I\!D, \text{ as } n \to \infty) \tag{28}$$

where B is standard Brownian motion. $I\!D$ is the Skorohod space of càdlàg functions $[0,\infty) \to I\!R$, see [J-Sh 87, Ch. 6].

3) On the probability space $(\Omega, \mathcal{A}, P)$ which supports the iid pairs $(V^{f,i}, \mu^i)$, $i \geq 1$, of subsection 3.2, we focus on the membrane potential processes $(A_t^{f,i})_{t\in[0,T]}$. Introduce filtrations in $\mathcal{A}$

$$\mathcal{G}^N = \left(\mathcal{G}_t^N\right)_{t\in[0,T]}, \quad \mathcal{G}_t^N = \bigcap_{r>t} \sigma\left(A_s^{i,f} : s \leq r, 1 \leq i \leq N\right), \quad t \in [0,T]$$

related to neurons $1 \leq i \leq N$.

4) We lift all processes, sub-σ-fields ... considered so far to the product space

$$(\widetilde{\Omega}, \widetilde{\mathcal{A}}, \widetilde{P}), \quad \widetilde{\Omega} := \Omega \times \Omega_1, \quad \widetilde{\mathcal{A}} := \mathcal{A} \otimes \mathcal{A}_1, \quad \widetilde{P} := P \otimes P_1.$$

We will use the following filtrations $I\!F^N$ in $\widetilde{A}$:

$$I\!F^N = \left(\mathcal{F}_t^N\right)_{t\geq 0}, \quad \mathcal{F}_t^N = \mathcal{G}_T^N \bigvee \widehat{\mathcal{F}}_t^N, \quad t \geq 0.$$

Thus on $(\widetilde{\Omega}, \widetilde{\mathcal{A}}, \widetilde{P})$, for every N, the martingale properties of B_N hold with respect to $I\!F^N$, and all variables $\Phi_N(r)$, $r \in [0,T]$, are $I\!F^N$-stopping times. Write $E := I\!R^2$ and consider on $(\widetilde{\Omega}, \widetilde{\mathcal{A}}, \widetilde{P})$ the sequence of E-valued processes

$$X_N := \left(B_N \circ \Phi^f, \widetilde{W}^N\right), \quad N \geq 1$$

with $\widetilde{W}^N = \sqrt{N}\left(\Phi_N - \Phi^f\right)$ as in 5.1. Since by construction on $(\widetilde{\Omega}, \widetilde{\mathcal{A}}, \widetilde{P})$ the processes B_N and Φ_N are independent, since Φ^f is a deterministic function, we have

$$B_N \circ \Phi^f \text{ and } \widetilde{W}^N \text{ are independent under } \widetilde{P}, \text{ for every } N. \tag{29}$$

Combining (28), (29) and step 2) of the proof of proposition 5.1, we have convergence of finite dimensional distributions of X_N to those of the E-valued process

$$X := \left(\sqrt{\lambda} \cdot B \circ \Phi^f, \widetilde{W}\right), \quad \text{with } B \text{ and } \widetilde{W} \text{ independent}$$

where B is the standard Brownian motion of (28), and $\widetilde{W}$ the Gaussian limit process of 5.1. Also we get from (27), (29) and step 3) of the proof of proposition 5.1

$$E\left(|X_N(t)|^2\right) = \lambda \cdot \Phi^f(t) + \widetilde{K}(t,t) = E\left(|X(t)|^2\right), \quad N \geq 1.$$

So all assumptions of [C-K 86, theorem 2] are satisfied, and we get

$$X_n \longrightarrow X \quad \text{(weak convergence in } \mathbb{L}_E, \text{ as } N \to \infty).$$

5) We turn to the processes $\sqrt{N}\,(\Psi_N - \lambda\Phi_N)$ in the assertion of proposition 5.2. For every $N \geq 1$,

$$\left(\sqrt{N}\,(\Psi_N - \lambda\Phi_N)\,,\, \Phi_N,\, \widetilde{W}^N\right) \quad \text{on } (\Omega, \mathcal{A}, P)$$

is equal in law to

$$\left(B_N \circ \Phi_N,\, \Phi_N,\, \widetilde{W}^N\right) \quad \text{on } (\widetilde{\Omega}, \widetilde{\mathcal{A}}, \widetilde{P}).$$

We will work on $(\widetilde{\Omega}, \widetilde{\mathcal{A}}, \widetilde{P})$. Fix some $t \in [0, T]$. With $\Phi_N(t)$ also

$$\sigma_N := \Phi_N(t) \wedge \Phi^f(t), \quad \tau_N := \Phi_N(t) \vee \Phi^f(t)$$

are $\mathbb{F}^N$-stopping times. B_N is a square integrable $\mathbb{F}^N$-martingale, hence on $(\widetilde{\Omega}, \widetilde{\mathcal{A}}, \widetilde{P})$

$$\begin{aligned} E\left(\sup_{r \in [[\sigma_N, \tau_N]]} |B_N(r) - B_N(\sigma_N)|^2\right) &\leq cE\left(\langle B_N\rangle_{\tau_N} - \langle B_N\rangle_{\sigma_N}\right) \\ &= c\lambda \cdot E(\tau_N - \sigma_N) \end{aligned}$$

for some constant $c > 0$. The last expectation vanishes as $N \to \infty$, by dominated convergence: first, the strong law of large numbers gives

$$\Phi_N(t) \longrightarrow \Phi^f(t) \quad \widetilde{P}\text{-a.s. as } N \to \infty, \text{ for every } t \in [0, T],$$

second, by definition of the processes $A^{i,f}$, one has

$$\tau_N - \sigma_N = \left|\Phi_N(t) - \Phi^f(t)\right| \leq T, \quad \text{for all } N \geq 1 \text{ and all } t \in [0, T].$$

Thus we have proved that for arbitrary $t \in [0, T]$ fixed

$$B_N \circ \Phi_N(t) = B_N \circ \Phi^f(t) + o_{\widetilde{P}}(1), \quad N \to \infty.$$

6) As a consequence of the last assertion, finite-dimensional distributions of the processes $B_N \circ \Phi_N$ and $B_N \circ \Phi^f$ coincide asymptotically as $N \to \infty$. Proceeding now in analogy to step 4) above, we obtain

$$\left(B_N \circ \Phi_N,\, \widetilde{W}^N\right) \longrightarrow X = \left(\sqrt{\lambda} \cdot B \circ \Phi^f,\, \widetilde{W}\right) \quad \text{(weakly in } \mathbb{L}_E, \text{ as } N \to \infty). \tag{30}$$

Using again the beginning of step 5), (30) implies the assertion of proposition 5.2. The proof ist finished. □

5.1. Proof of theorem 3.5

With notations of the preceeding proof, for every N, the process

$$\sqrt{N}\left(\Psi_N - \lambda\Phi^f\right) = \sqrt{N}\left(\Psi_N - \lambda\Phi_N\right) + \lambda \cdot \sqrt{N}\left(\Phi_N - \Phi^f\right) \quad \text{on } (\Omega, \mathcal{A}, P)$$

is equal in law to

$$B_N \circ \Phi_N + \lambda \cdot \widetilde{W}^N \quad \text{on } (\widetilde{\Omega}, \widetilde{\mathcal{A}}, \widetilde{P}).$$

For $E = \mathbb{R}^2$, the mapping $\mathbb{L}_E \ni (g_1, g_2) \to g_1 + g_2 \in \mathbb{L}_{\mathbb{R}}$ is continuous. So the continuous mapping theorem combined with (30) gives

$$B_N \circ \Phi_N + \lambda \cdot \widetilde{W}^N \longrightarrow W := \sqrt{\lambda} \cdot B \circ \Phi^f + \lambda \cdot \widetilde{W} \quad \text{(weakly in } \mathbb{L}_{\mathbb{R}}, \text{ as } N \to \infty)$$

with B and $\widetilde{W}$ independent. Hence weak convergence in $\mathbb{L}_{\mathbb{R}}$

$$\sqrt{N}\left(\Psi_N - \lambda\Phi^f\right) \longrightarrow W, \quad N \to \infty$$

is proved. This concludes the proof of theorem 3.5.

We remark that we do have convergence of finite-dimensional distributions, i.e. exceptional set $N = \emptyset$ in i)+ii) following (24), as a consequence of (29) and step 5) of the proof of 5.2. □

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