History of neuroscience of self-initiated action and volition: recent developments and paradigm shift

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Abstract

For decades several studies have been trying to find the **source of 'intention' in the brain**. Historically, we have two landmark studies. The first one, by Kornhuber and Deecke (1965) lead to the **discovery of the readiness potential (BP)**, a slow buildup of neural activity preceding un-cued, "self-initiated" movements, whose location was identified in the preSMA and SMA areas of the brain. This buildup has been observed using both invasive and non- invasive neural recordings and in both vertebrate and invertebrate species.

Around 20 years later, the experiment by Benjamin Libet (1983), showed a lag between the subjective time of the urge or intention to move and the neural decision to act represented by this electrophysiological signal of movement preparation, opening up a still running debate concerning the **unawareness of neuronal mechanisms underlying free choices**. In this panorama, the research on self-initiated action has so far proceeded under the **assumption** that this buildup reflects the beginning **of a causal process** of "planning and preparation for movement".

Recent developments in the field seriously challenge this assumption and have opened the door to a **paradigm shift** in this area of research. We will review the modern history of research on self-initiated movement and volition with a focus on these recent developments, suggesting how the **introduction of formal computational models** (accumulator or bounded-integrator models) for the study of volition is playing a major role in this change of perspective.

Definitions

Self-initiated movements

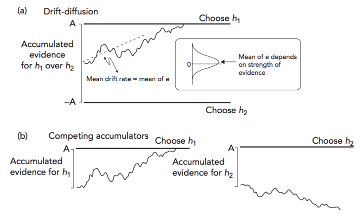
Actions/movements are self-initiated/generated 'if *not uniquely* specified by external cues', **as opposed to externally triggered movements/actions**. Pressing on the brake pedal when the traffic light ahead turns red is an example of an action initiated in response to a sensory cue. Deciding whether and when to kick a football, instead, leads to one of those actions that from a third-person perspective appear to be both **voluntary and spontaneous**, and are commonly referred to as 'self-initiated'.
For an extensive review on the topic and the debate around the definition of self-generated actions see Schüür & Haggard 2011

Neural decision to move

A neural event or state that commits the motor system to the initiation of an imminent movement in a specific moment. As Schurger et al. 2016 points out, "it is not necessary for this state to be conscious for it to qualify as a 'decision'".

Integration-to-bound or evidence accumulator models

A class of computational models of decision making (fig. 1) where external sensory evidence (=signal) and internal neural activity (= Gaussian noise) are **integrated over time towards a decision-threshold** which, crossed, leads to the motor response. In the case of spontaneous self-initiated movement the sensory evidence is absent or weak and replaced by internal noise.



[Fig. 1, adapted from Haggard in Mele 2015]

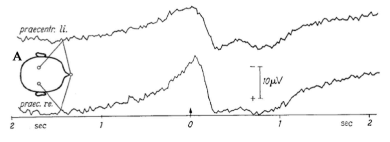
History (1): discovery of the *Beireitschaftpotential ~60's*

In 1965 Kornhuber & Deecke report the discovery of slowly increasing surface-negative brain potentials (fig.2) accompanying voluntary movements of the limbs. These are called *Readiness Potentials* and considered the 'electrophysiological sign of planning, preparation, and initiation of volitional acts' (Kornhuber & Deecke 1990).

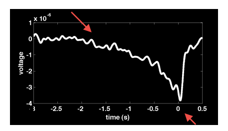
In an experimental context dominated by conditional reflex studies on sensory-evoked potentials (cfr. the '**expectancy wave**' or **CNV**, discovered 1 year before by Walter et al. 1964), this is the first experimental evidence that 'the willingness to act' is independent of preceding sensory stimulation.

Somehow, the name itself suggests the implicit idea that this buildup of activity is presumed to reflect a **preparatory process** that is causally responsible for the decision of producing a movement.

Paradigm: participants were instructed to execute repetitive hand/foot movements by pressing a button for 100-500 times in irregular intervals with pauses of at least 15 s.



[Fig. 2, adapted from Kornhuber & Deecke 2016]



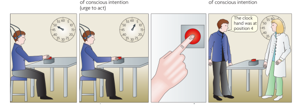
[Fig.3, schematic of RP]

History (2): the 'Libet paradox' ~80's

In 1983 Libet introduces a variable to the classical Rp paradigm: the 'time of conscious intention to act' (called reportable time or Wt) is studied in relation to the onset of cerebral activity that precedes 'freely voluntary, fully endogenous motor act'.

Paradigm (fig.3): participants were asked to make a spontaneous movement (abrupt flexion of finger or wrist) after a **complete rotation of a monitoring clock** at any time when they felt the 'urge' to move, without preplanning when to act and to report after the recalled clock-position coinciding with the **moment of subjective awareness of 'wanting' or intending to act (W)**. Subjects were also required to report the time of awareness of actually moving (M) and the time of awareness of a tactile sensation (S) delivered on the back of their hand at irregular unknown times.

The striking result was that the onset of the RP was shown to precede the reported time of conscious intention to act by 300-up to 800ms. This finding had important philosophical consequences by leading the prevalent (dualist) view that the brain unconsciously initiates decision processes that only at the end come to consciousness. In Libet's words: "**the brain 'decides'** to initiate or, at least, to prepare to initiate the act before there is any reportable subjective awareness that such a decision has taken place"



[Fig.4, adapted from Haggard 2008]

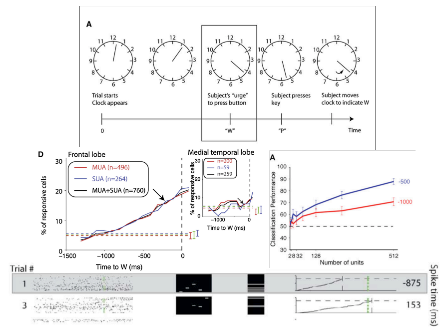
On the nature of the RP *~70's-2000's*

Many other studies replicated the RP paradigm showing both in normal and pathological condition **factors that can influence its magnitude and time course** [for a review Di Russo et al. 2016, Shibasaki & Hallett 2006,].

Two main functional components of the RP are found (fig.4), the **Early BP and the Late BP** which originate from different cortical sources (pre-SMA/SMA, M1) [see Shibasaki & Hallett 2006]

Studies on non human animals, vertebrates and invertebrates (monkey, rat, crayfish) show the universality of this brain signal [cfr. the 'readiness discharge' in Kagaya & Takata 2011, 2010].

Fried et al. 2011: a study in between 2 paradigms



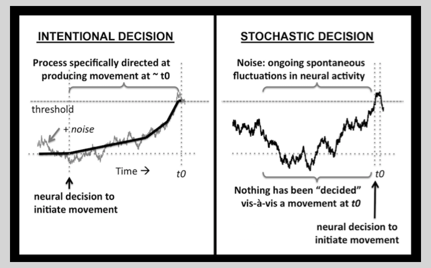
[Fig.5-8 adapted from Fried et al. 2011]

The Libet paradigm is replicated with single unit recording in the human brain (fig.5). Evidence that preconscious activity of 256 SMA neurons not only **precedes volition** (W reports) but can also **predict** with >80% of accuracy **volition** already 700 ms before subjects' awareness.

Implementation of a **integration-to-fire model** (fig.6) that explains the emergence of the 'feeling of will' as the integration of firing rate crosses a threshold.

The buildup of activity as the **consequence of a neural decision** to move?

2 interpretations of the RP ~ *2010's*

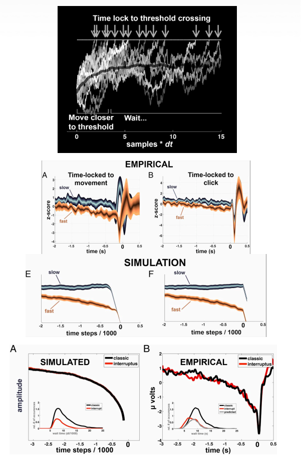


Schurger 2012: noise integration & paradigm shift

Subjects are tested in a variation of the Libet task, the 'Libetus Interruptus task', where while performing spontaneous action initiations they can be unexpectedly interrupted by random auditory clicks (an imperative to act) and be asked to anticipate their movements.

The **leaky stochastic accumulator model** predicts that earlier responses might correspond to moments in which spontaneous brain activity is closer to the decision threshold and that **an imperative to act can shift premotor activity closer to threshold.**

The gradual exponential-looking increase in neuronal activity can be obtained through the **average of stochastic subthreshold fluctuations** in brain activity time locked to movement onset (fig. A).
Thus, the buildup of activity **cannot be 'caused' by the neural decision** to move.



[Fig. 9-12 adapted from Schurger et al. 2012]

Conscious intention & free will ~ *80's-2000's*

Debate: the psychologist William Banks (2006) wrote that "free will seems pointless if it is not conscious free will. We are not interested in unconscious freedom of the will, if there is such a thing"[from Mele A.R. 2015].

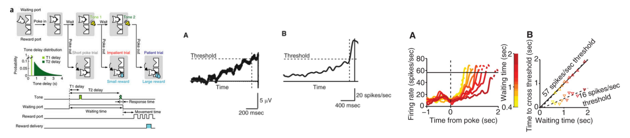
Critiques on Libet's methodology (reliability of participants' subjective report) but main results replicated (e.g. Fried et al. 2011, Haggard & Eimer 1999).

Controversy on whether the RP reflects specific or non-specific premotor processes : lateralised readiness potential (LRP) as a better indicator of motor preparation. Cfr. Alexander et al. 2016.

Integration-to-bound models for spontaneous action initiation studies *~ 2010's*

The convergence of empirical studies and computational modelling has become an established trend in many neuroscience domains of research. In particular, in the field of volition the study of spontaneous action initiation benefits from the novel introduction of bounded integrator models, traditionally dominant in decision making.

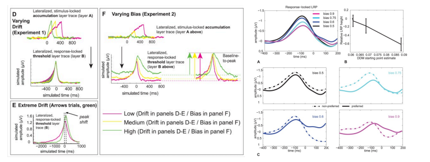
After Schurger et al. 2012 another important experimental study conducted on rats by Murakami et al. 2014 has strengthened the evidences supporting the explanatory power of this class of models for spontaneous self-initiated movements.



[Fig. 13, 15, adapted from Murakami et al. 2014] [Fig. 14, schematic adapted from Rigato et al. 2015]

Rats are tested in a waiting task where a different amount of reward is proportionally delivered as a function of how much the rat waits. Giving up trials (the ones where rats abort waiting) are considered as spontaneous actions. An **integrator-model** rating activity of neurons -recorded in rat M2 during spontaneous giving up trials- is accumulated towards the threshold and will only be decisive for the action initiation when the threshold is crossed (fig. 9). The ramping activity of this population of neurons resembles the integrated evidence in lateral intra-parietal area.

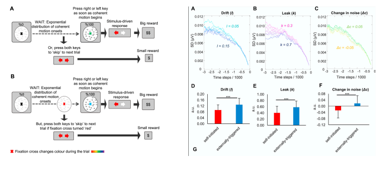
Van Vugt et al. 2014 show how the dynamic of a decision threshold crossing can be reflected also by the lateralized readiness potentials (LRPs). Using a Drift-Diffusion Model they predict and find a correlation between the amplitude and shape of the early part of the LRP and the rate of evidence accumulation of participants performing a motion discrimination task (fig. 16, 17).



[Fig. 16-17 adapted from Van Vugt et al. 2014]

A recently published study by Khalighinejad et al. 2017 re-adapts the leaky stochastic decision model to account for trial-to-trial variability of participants' RP, predicted to progressively decrease before self-initiated actions in a skipping response paradigm. The new model validates the main findings by Schurger et al. 2012 by showing a substantial difference in the integration of internal noise in the self-initiated vs externally-triggered conditions with the additional assumption of noise reduction.

[Fig. 18-19 adapted from Khalighinejad et al. 2017]



*Gluth et al. 2013 also conduct a study on RP & LRP adopting an accumulator model, but since their study is purely based on a decision making task it was not examined here.

Perceptual-decision paradigms for SVM studies ~ *2010's*

The introduction of computational model in the study of spontaneous action initiation has been accompanied by another very recent change in the experimental paradigms in the domain of volition. As extensively discussed by Khalighinejad et al. 2017, in traditional readiness potential paradigms -such as the Libet task- the experimenter asks participants to '**act freely**', i.e. to initiate a movement whenever s/he feels like/the urge to move. This top-down **instruction of 'being spontaneous'** is spurious and paradoxical.

Novel studies then have adopted '**reward-guided perceptual decision making' paradigms** (and in particular **inter-temporal choice tasks**) as more ecological candidates to trigger endogenous actions.
Murakami et al. 2014 and Khalighinejad et al. 2017 implemented tasks where the motor response ('skip response' or 'giving up waiting') is elicited in a randomly long foreperiod thus resembling the transition between inaction-action present in animal **foraging behaviour**.

Conclusions

We tried to provide an historical account of the main studies in the field of self-initiation and volition, with a central focus on the discovery and the study of the Readiness Potential. In particular we propose **two main parallel directions of the research**, in the footsteps of the work by Kornhuber & Deck (1965) and Libet et al. (1983): one investigating more closely the nature of this electrophysiological signal and another one intermingling with the studies on consciousness. We then highlight how a **radically innovative interpretation of the RP** is marking a change in paradigm between the classical studies and the recent approaches, not only **from the theoretical point of view** but also **from the methodological one** with the introduction of bounded-integration models and choice tasks from decision making studies.

References

Alexander P., Schlegel A., W. Sinnott-Armstrong et al. (2016), *Readiness potentials driven by non-motoric processes*, Conscious Cogn. 39: 38-47.

Di Russo F., et al. (2016), *Beyond the 'Bereitschaftspotential': Action preparation behind cognitive functions*, Neurosci Biobehav Rev. 78:57-81.

Fried I., Mukamel R., Kreiman G. (2011), *Internally generated preactivation of single neurons in human medial frontal cortex*, Neuron 69: 548-562.

Gluth S., Rieskamp J., Büchel C. (2013), *Classic EEG motor potentials track the emergence of value-based decisions*, Neuroimage. 79:394-403.

Kagaya K., Takahata M. (2011), *Sequential synaptic excitation and inhibition shape readiness discharge for voluntary behavior*, Science 332(6027):365-8.

Kagaya K, Takahata M. (2010), *Readiness discharge for spontaneous initiation of walking in crayfish*, J Neurosci.;30(4):1348-62.

Khalighinejad N., Schurger A., Desantis A., Zmigrod L., Haggard P. (2017), *Precursor processes of human self-initiated action*, Neuroimage 165:35-47.

Kornhuber H.H.,Deecke L.(2016), *Brain potential changes in voluntary and passive movements in humans: readiness potential and reafferent potentials*, Pflugers Arch - Eur J Physiol, 468 (1115).

Haggard P. (2008), *Human volition: towards a neuroscience of free will*, Nat. Rev. Neurosc., 934-46.

Haggard P., Eimer M. (1999), *On the relation between brain potentials and the awareness of voluntary movements,* Exp Brain Res. 126(1):128-33.

Libet B., Gleason C.A., Wright E.W., Pearl D.K(1983), *Time of conscious intention to act in relation to onset of cerebral activity (readiness-potential). The unconscious initiation of a freely voluntary act*, Brain,106:623-42.

Mele A.R. , edited by (2015), *Surrounding free will - philosophy, psychology, neuroscience*, Oxford University Press.

Murakami M.,Vicente M.I., Costa G.M., Mainen Z.F. (2014), *Neural antecedents of self-initiated actions in secondary motor cortex*, Nat Neurosci. 17(11):1574-82.

Rigato J., Murakami M., Mainen Z. (2015), *Spontaneous Decisions and Free Will: Empirical Results and Philosophical Considerations,* Cold Spring Harb Symp Quant Biol. 79:177-84.

Schurger A., Mylopoulos M., Rosenthal D. (2016), *Neural Antecedents of Spontaneous Voluntary Movement: A New Perspective*, Trends Cogn Sci, 20(2):77-79.

Schurger A., Sitt J., Dehaene S.(2012), *An accumulator model for spontaneous neural activity prior to self-initated movement*, PNAS, 109(42).

Schüür F., Haggard P. (2011),*What are self-generated actions?*, Conscious Cogn. 4:1697-704.

Shibasaki H., Hallett M.(2006), *What is the Bereitschaftspotential?*, Clin Neurophysiol.,117(11):2341-56.

Walter W.G. 1964), *Slow potential waves in the human brain associated with expectancy, attention and decision,* Arch Psychiatr Nervenkr. 206:309-22.

Van Vugt M.K., Simen P., Nystrom L., Holmes P., Cohen J.D. (2014), *Lateralized readiness potentials reveal properties of a neural mechanism for implementing a decision threshold,* PLoS One 13;9(3).

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