Marco Capogna, a pioneering neuroscientist and true European

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Abstract

Marco Capogna PhD, Professor of Neuroscience at Aarhus University Faculty of Health, Department of Biomedicine, Aarhus, Denmark, died from cancer aged 64 on 2nd December 2022.

Obituary - Marco Capogna (1958 - 2022)

"A pioneering neuroscientist and true European"

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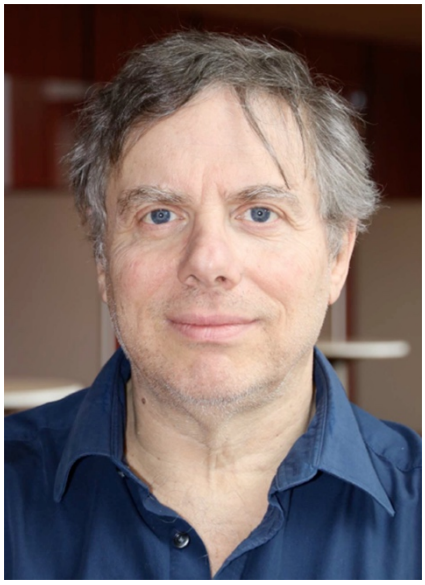

Fig. 1. Marco Capogna
Roma 1958 – Aarhus 2022.

Marco Capogna was born in Rome (Fig. 1), Italy in 1958. He studied Experimental Psychology at the University of Rome and Biology at the University of Pisa. Marco was then drawn to neuroscience and undertook a PhD at the Dept. Physiology and Biochemistry G. Moruzzi of the University of Pisa, where he performed experimental studies with Walter Francesconi and Marcello Brunelli on the excitability of neurons in the frontal cortex of rodents. After receiving his PhD in 1992, he joined the research group of Dr Scott Thompson and Prof Beat Gähwiler for a postdoctoral fellowship at the University of Zurich, Switzerland.

Scott Thompson remembers the Zurich years: Marco was my first postdoc - How lucky was that!

He joined my laboratory at the Brain Research Institute of the University of Zurich in the group of Prof Beat Gähwiler in 1992, after completing his PhD. He then stayed on as a postdoc until just after I left in 1998. During this time, Marco was one of the most

productive, stimulating, pleasant, and enthusiastic collaborators I have ever been fortunate enough to work with.

In my laboratory, Marco performed a number of important studies concerning the regulation of neurotransmitter release from presynaptic nerve terminals in the hippocampus, taking full advantage of the slice culture technique invented by Beat [43]. In particular, we were interested in the mechanism by which presynaptic G protein-coupled receptors and protein kinases change neurotransmitter release. At a time when modulation of presynaptic voltage-dependent channels was the dominant hypothesis, Marco's hard work provided strong evidence of an unexpected second process - direct modulation of synaptic vesicle fusion [26,29,65,70]. Although the data were incontrovertible, the conclusion was controversial and elicited a passionate scientific back-and-forth lasting several years. Ultimately, Marco's work persuaded many to his point of view. In the course of these studies, Marco became interested in the mechanisms of action of several neurotoxins that affect transmitter release, including clostridial toxins and latrotoxin, and made some of the first careful, systematic investigations of their physiological actions in the mammalian CNS [27,28,31]. All of Marco's contributions to this field are characterized by extreme thoroughness and rigor and have been rewarded with recognition and respect. He also contributed to other on-going studies in the laboratory and was widely appreciated as a collaborator by the whole team.

In the blissful era before emails took up hours a day of everyone's attention, Marco was devoted to recording, spending many long hours at the rig – the key to success for an electrophysiologist. My rig was in the same lab and we kept a cheerful banter up all day. My knowledge of Italian improved considerably. Particularly, swearing at electrodes and cells - common practice amongst electrophysiologists - including in his native Roman slang. His productivity was outstanding by all measures, not only number of publications, but more importantly, in terms of sustained scientific impact. His work comprises a large number of my most highly cited papers.

Beat's group was teeming with talented neurophysiologists in those wonderful years: Etienne Audinat, Serge Charpak, Dominique Debanne, Kobi Fischer, Urs Gerber, Natalie Guérineau, Thomas Knöpfel, Anita Lüthi, Anne McKinney, and Massimo Scanziani. We were a tight knit crew in and outside of the lab, sharing many a practical joke, as well as non-stop passionate arguments over science. It was the best of times for all of us. For Marco, his love of Teresa was formed in those years. We

all knew something was very different for Marco when they started dating. He was a little less dishevelled and his smile was even bigger than normal! He even gave up playing classical guitar. As he told me at the time, “If I can’t practice three or four hours a day, I can’t play at the level I expect to play. I’d rather spend those hours with Teresa!” He will be missed!

Subsequently, Marco Capogna moved to the UK as a senior scientist at the Novartis Institute for Medical Sciences of University College London in 1999. In January 2001, he joined the MRC Anatomical Neuropharmacology Unit (ANU) at the Department of Pharmacology of the University of Oxford.

Peter Somogyi remembers in Oxford: Longing for the freedom to explore his ideas he was very keen to move back into academic research from industry. I remember how already in the first interview for a group leader position in the MRC ANU (Fig. 2) at the Department of Pharmacology his insuppressible curiosity shone through, which got him the job. He set up his electrophysiology laboratory on the same floor next to mine and we shared a histological laboratory. Marco enjoyed the lively flow of expertise and ideas amongst the groups in the Unit; all groups were small, facilities were shared and people thrived. Marco developed his distinct synaptic pharmacology research programme focussing on the roles of GABAergic neurons and presynaptic receptor modulation of transmitter release in the hippocampus testing various disease models in rodents. We met almost daily and took stock of progress in the six monthly Science Days, where all ongoing work was displayed, discussed and dissected, ending with a joint dinner. Marco was a highly critical, but kind discussant in these meetings.

After his arrival he focussed on the hippocampus building on his extensive experience from his days in Zurich. Amongst the many original observations he published, the series of papers on the origin and mechanisms of slow GABA-mediated inhibition by neurogliaform cells and its consequences for operation of hippocampal circuits are remarkable. With postdoctoral scientist Chris Price, they demonstrated that feedforward inhibition evoked by the perforant pathway from the entorhinal cortex activated a novel network of electrically and synaptically connected neurogliaform cells, which evoked both unitary GABA-A and GABA-B receptor-mediated responses in postsynaptic pyramidal cells and interneurons [62,64]. With doctoral student Theofanis Karayannis they established that in the hippocampus the firing of neurogliaform cells generates a prolonged low concentration of GABA, responsible for

the slow GABA-A receptor-mediated current and a robust receptor desensitisation and use-dependent synaptic depression, which they could also evoke by injecting in vivo recorded firing patterns into single neurons [48,49].

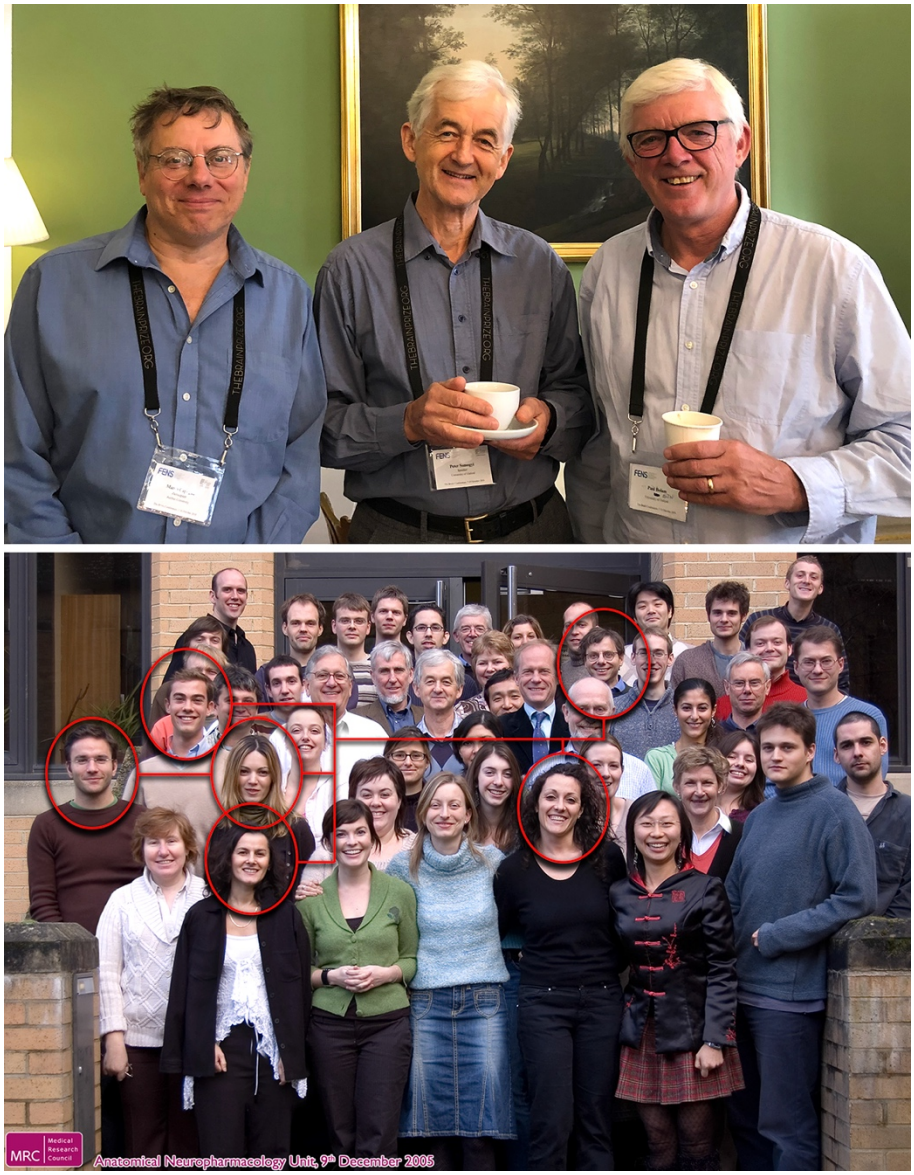

Fig. 2. Top, FENS meeting, Copenhagen 18th Oct. 2018. From left: Marco Capogna, Peter Somogyi and Paul Bolam. Bottom, 2005 MRC ANU Science Day. Marco Capogna and his research group in frames. From top right: Marco Capogna, Raffaella Geracitano, Tatjana Lalic, Romana Hauer, David Elfant and Theofanis Karayannis.

With doctoral student Gengyu Li they demonstrated that the firing pattern of neurogliaform cells recorded *in vivo* by Thomas Klausberger induces self-inhibition of transmitter release via a nitric oxide mediated presynaptic mechanism [54]. Subsequently, with doctoral students Miroslawa Manco and Thomas Bienvenue they discovered the firing, slow synaptic dynamics and synaptic connections of

neurogliaform cells in the baslolateral amygdala (BLA) as well [56]. I was fortunate to collaborate with Marco on many occasions, including the extension of his work on neurogliaform cells to related neurons in all layers of the hippocampus, which with Thomas Klausberger we named the *ivy cells* [42]. Right through his tenure in the Unit, Marco was fascinated by the regulatory roles of multiple presynaptic receptors on single nerve terminals. For example, in the perforant path glutamatergic pathway from the entorhinal cortex, with Chris Price they showed that group II metabotropic glutamate receptors (mGluRs) act via dendrotoxin-sensitive potassium channels, whereas group III mGluRs are coupled to N-type calcium channels, governing transmitter release with different temporal dynamics in interneurons [63].

His interest gradually turned to the amygdala and the role of defined cell types and circuits in fear conditioning and related synaptic plasticity mechanisms. With Marie Curie Fellow Raffaella Geracitano and his friend the previous Unit member, Francesco Ferraguti (Innsburck), they established the synaptic properties of intercalated paracapsular GABAergic neurons, which are specific to the amygdala and key elements in fear learning [45]. Subsequently, based on his work on the hippocampus, Marco predicted and proved that many of the same GABAergic neurons that provided temporo-spatial structure in the hippocampus were also present in the basolateral amygdala (BLA). In a landmark study with doctoral student Thomas Bienvenu they identified the *in vivo* network oscillation-related firing patterns of distinct GABAergic neurons and their synaptic relationships. They discovered that salient sensory stimulation selectively activated axo-axonic cells, which innervate the axon initial segments of the glutamatergic principal projection neurons that distribute outputs to the rest of the brain [6]. In contrast, another distinct type of GABAergic projection neuron was inhibited by the same stimulus. They proposed that the time-, target domain- and sensory-specific release of GABA cooperates in promoting amygdalo-hippocampal dialogue and emotional memory formation [6]. In the same series of experiments with Bienvenue and Francesco Ferraguti they also discovered a population of large intercalated GABAergic neurons that widely projected in the brain in addition to innervating other GABAergic neurons in the BLA [7]. Nociceptive stimulation strongly activated these cells via the thalamus. They proposed that large intercalated neurons evoked disinhibition of principal neurons in multiple target areas, coordinating their activity and the animal's response [7]. Marco continued his work of identifying neurons in the amygdala after he moved to Aarhus University.

Following the closure of the ANU in 2015, the directors of the new Brain Network Dynamics Unit, that took over the work developed in the ANU, did not wish Marco to continue. We were both fortunate to obtain a joint ERC grant in 2015 for exploring cellular diversity and synaptic interactions in the human cerebral cortex in vitro in surgical samples, before Marco moved to Aarhus University in Denmark to take up the post of Professor of Neuroscience. Our continued collaboration was facilitated by this grant. We enjoyed the beauty of the organisation of the human cortex and Marco's extensive experience with brain slices and cultures helped to solve the many initial challenges. We also helped each other in frustrating periods when facing regulatory red-tape and the obstacles created by the Covid-19 pandemic. Our grant finally terminated on the 30th of November 2022, just two days before Marco passed away.

Felipe Fredes and colleagues* remember in Aarhus: In 2016, Marco moved to Denmark as a Professor at the Department of Biomedicine, Aarhus University. He naturally integrated into the Danish neuroscience society as well as into Danish research institutes (DANDRITE, PROMEMO) providing expertise in neurophysiology and also contributing to neuroscience education in Denmark. He was very active in bringing international researchers from across the globe (Fig. 3), and he always took great care to make sure everyone felt at home in Aarhus.

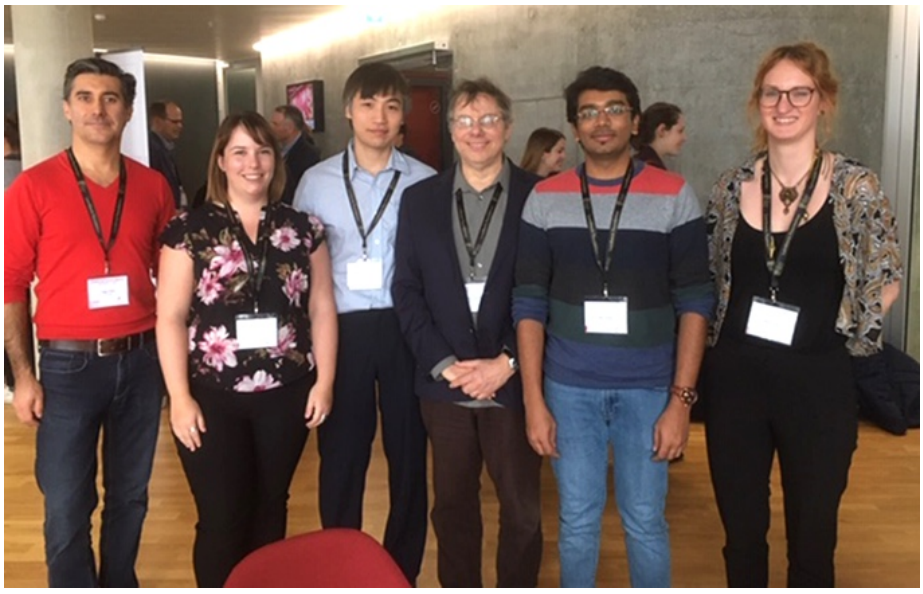

Fig. 3. 2019 "Proteins and Circuits in Memory" Meeting, Copenhagen. From left: Felipe Fredes, Emma Louth, Wen-Hsien Hou, Marco Capogna, Meet Jariwala and Meike Claudia Sieburg.

He continued to pursue his interests in characterizing novel GABAergic cell types in the mouse limbic system, identifying the roles of such neurons in the rodent amygdala in sleep homeostasis and memory engram formation. In parallel, he bridged basic and clinical neuroscience research by establishing collaborations with Aarhus University Hospital and the neurosurgery team.

With his colleagues he used living human brain samples from tissue removed during tumour surgery and studied synaptic mechanisms in the cerebral cortex. With postdoctoral scientist Emma Louth, they observed that the activation of dopamine receptors modulated spike-timing-dependent glutamatergic synaptic plasticity differently in cortical pyramidal cells of mice and humans [55]. In the human cortex, dopamine converted long term synaptic depression evoked by a stimulation protocol into long term potentiation. His last efforts were dedicated to investigating cell-type specific GABAergic synaptic plasticity in the human neocortex using organotypic slice cultures and viral labelling of defined types of cortical interneurons.

To those who worked in his lab in Aarhus, he was much more than a mentor. His optimism and passion for science were an inspiration to everyone as he would regularly participate in late-night electrophysiology experiments, even finding time to patch a few human neurons himself, or in early morning watching the sleep recordings of freely moving mice. For those who worked with him as fellow faculty, he was also much more than an academic colleague. He always shared his warm support and friendly and constructive critique, and he would gladly step in when colleagues were in need of a helping hand. He saw it as his great joy to connect local colleagues to his international network. His torch will be carried by the next generation throughout the globe.

Francesco Ferraguti remembers in Innsbruck: although we had met earlier at scientific meetings, I got to know Marco well when he joined the MRC ANU in Oxford. The highly collaborative atmosphere of the Unit helped to fire up our scientific interaction, which then developed into a very close professional partnership and deep friendship through the years. During our overlap in Oxford, we used to spend a lot of time together within and outside the lab. Marco was very much a polymath, with a deep knowledge about music, art, literature and politics, hence our discussions, generally starting from scientific matters often branched out to all sorts of topics. We also enjoyed spending time in outdoor activities. We went running and played tennis together. I remember with a certain wistfulness the tennis games on the grass courts of the Oxford

University park, when occasionally we challenged in doubles his students Theo Karayannis and David Elfant having great fun together.

When in 2002 it became clear that I had to leave the Unit and I could start my own lab in Innsbruck, I decided to focus on the neural bases of negative emotions. The high translational value of Pavlovian fear conditioning particularly appealed to me, a behavioural paradigm tightly related to precise cortical circuits, which could offer great potential to explore the fundamentals of the neurobiology of emotions. Central to this form of associative learning is the amygdaloid area, whose operational principles were at the time still poorly understood. I shared these ideas with Marco and he enthusiastically accepted to jointly investigate the diversity of GABAergic neurons in the amygdala and their involvement in fear learning. We could capitalize on our complementarity and the strong tradition of the Unit in exploring neuronal diversity and circuit operations in other cortical areas.

Fig. 4. 2015 IBRO Meeting, *"Circuit dynamics of the hippocampal-amygdala network and their alterations in stress and anxiety disorders"* Symposium, Rio de Janeiro. From left: Francesco Ferraguti, Daniela Kaufer, Marco Capogna and Sumantra Chattarji.

One of our main shared achievements has been the elucidation of some of the key structural and functional features of the intercalated cell masses of the amygdala [7,17,44,45]. Marco's work has been instrumental in defining several types of BLA interneurons and their role in shaping BLA activity in relation to hippocampal oscillations (Fig. 4) and noxious stimuli, two processes critical for forming emotional

memories [6]. Marco himself commented that "*with a number of international colleagues, over the years, we collected data showing an astonishing diversity of GABAergic neuron types and their specific roles in the healthy and pathological brain. I believe this has been my major contribution to Neuroscience*". He went on to reveal the cellular mechanisms mediating hippocampal gating of amygdala information processing related to fear learning [3]. It has been a real privilege to have worked with him on these projects and our almost weakly discussions on the data were a constant incentive. Our scientific partnership persisted also after he moved to Aarhus University. He invited me to team up with him and Cheng-Chang Lien (Taipei) to define a novel inhibitory engram in the central lateral amygdala. With his student Wen-Hsien Hou we were able to establish that an engram underlying fear memory is formed exclusively by a population of GABAergic neurons mostly expressing the neuropeptide somatostatin. We hope that this work, which is currently in revision, can soon be published to give further credit to Marco's scientific legacy.

Up to the very last day Marco fought with great dignity and courage against an evil that left him no escape. Despite the failure of the therapies, Marco never failed in his unshakeable faith in science; the only road that can lead one day to understand and cure diseases, saving lives. Our friendship kept us close until the end, here I mourn a special friend.

Marco always acknowledged the contribution of colleagues to his research achievements and was always generous with ideas and time to support the work of others. He was a brilliant scientist, intensely curious and an inspiration to all of us who worked with and learned from him. In his work, he had an exemplary intellectual rigour and ethical attitude, demonstrating the highest level of scholarship. In addition to his seminal scientific contribution, Marco will be remembered as a caring mentor who conveyed to his trainees and colleagues his engagement and great joy in doing science. Marco served on various boards and grant reviewing committees, and was a member of the editorial board of the European Journal of Neuroscience and eLife.

With his loving wife, Teresa Ariosto, a theatrical producer, he had two children Lidia and Flavio and enjoyed a harmonious family life. When not busy with professional or family activities he was happiest playing classical guitar, reading international literary classics and novels, in particular his favourite writer Elias Canetti.

Marco constantly looked closely at the Italian research landscape and was frustrated by the chronic policy of underfunding of research and education, which adversely affects Italian science. He was dismayed by the constant brain drain particularly of the most talented young scientists. He was one of them. He was a true European and valued the best of things in the countries in which he lived. He was hoping to see a united Europe without internal boundaries and not held back by nationalism, a really long-term project that did not happen in his life, but at least he witnessed some progress.

His death means an unbridgeable loss to his family. His memory will be treasured by his former colleagues and the international community of neuroscientists. He will be greatly missed, but his legacy will live on in the knowledge that he contributed to mankind and in the work of his students and those he had influenced.

Footnote: * Poul Henning Jensen; Poul Nissen; Anders Nykjaer

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