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Coding cognition

Representing and communicating information in perceptual and memory systems

Dorman, R.

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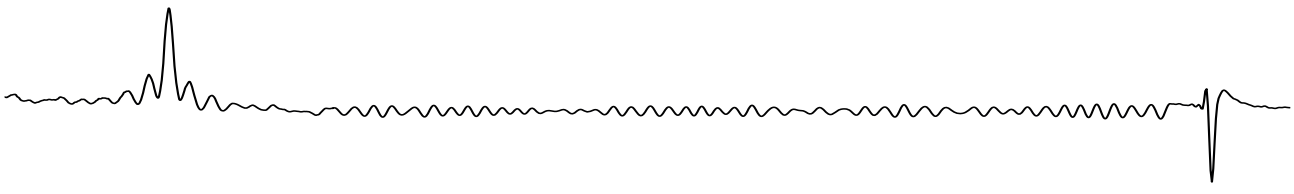
English Summary

Nederlandse samenvatting



English summary

The mammalian brain can perform astonishing cognitive functions. The computations by which the brain performs these functions run on networks of interacting neurons. The signals of communication in this network can be described with a neural code, which neuroscience aims to approximate through the various quantifiable measures of brain activity. In the field of neurophysiology, we can probe the electrical activity of groups of neurons during cognitive processes in awake behaving animals and correlate this behaviour with neuronal activity.

In this thesis, we first investigate correlations between action potential firing of individual neurons with the activity of entire populations (Chapter 2). This correlation provides us with a quantification of how well a particular neuron's spikes are coupled with activity in a certain area. We investigate this coupling within and between the visual cortex, the whisker fields of the somatosensory cortex, the perirhinal cortex and the CA1 region of the hippocampus, in the freely moving rat. We find different levels of coupling within the various areas, which correspond, at least in part, to the known physiological architecture of such areas, such as the synchronous firing in the hippocampal CA1 region. Furthermore, we find that coupling between different areas is less temporally precise compared to within-area coupling, presumably due to polysynaptic pathways between areas. Within-area and between-area coupling are generally positively correlated, especially for coupling between cell from the CA1 field and the other areas (visual cortex, somatosensory cortex and perirhinal cortex). Furthermore, we have identified 'broadcasting' units that show low levels of coupling with their local population but are strongly coupled to other regions. Furthermore, we put this metric of coupling in a cognitive context. First, we correlated spatial selectivity of neurons with coupling and found a negative correlation, notably in the CA1 region. We ascribe this negative correlation to the antithesis between the specificity necessary for high spatial selectivity, and the non-specificity associated with high population coupling. Secondly, we relate coupling with brain states such as wakefulness and sleep and find a decrease of within-area coupling in non-REM sleep, but generally preservation of coupling levels between areas in non-REM sleep, quiet wakefulness, and active states: only during non-REM-sleep do we find reduced coupling between CA1 neurons and different areas.

Secondly, in Chapter 3 we investigate phase-coding as a relevant parameter in neural coding. During a multisensory detection task in head-fixed mice, we investigate how single-neuron spikes in primary visual cortex (V1) correlate with phases of theta rhythm (~10 Hz) in the Local Field Potential. We find that a subpopulation of phase-locked neurons, who respond to visual and audiovisual stimulation, show changes in the preferred phase-of-firing with regard to the LFP between visual-only and audiovisual conditions given the same visual stimulus. Additionally, we find differences in the phase-of-firing distribution when presenting various visual stimulus orientations. These results match with the theoretical model in Pennartz (2009), describing how phase-coding might be necessary as an additional coding metric to appropriately code cross-

modal relational representations while being able to sustain a stable representation of visual features.

Lastly, we report on an important concept for properly interpreting a neural code: the knowledge of irrelevant signals in the data. Specifically, even in head-fixed mice, motor-related neuronal activity is found across the neocortex. In multisensory integration research, cross-modal sensory neural activity could potentially be 'contaminated' with activity elicited from motor behaviour. In Chapter 4 we correlate orofacial motion with neural activity during the same multisensory detection task used in chapter 3. We make use of a forced delayed-response window in said task and investigate whether the delay provides us with a window free of motor-induced activity. Spontaneous orofacial motion is decreased during the delay period, and after the delay period a strong increase in motor activity and related spiking activity of V1 neurons is seen. During the delay, salient auditory stimuli elicit orofacial motion and related neuronal activity. However, salient visual stimuli did not elicit a strong motor response in this period. Although visually selective neurons still show correlations with motor activity, we identified a subpopulation of visually responsive neurons carrying visual stimulus information, without correlating with the behavioral confounds.

These studies investigated several aspects of neural coding. The networks made up of neurons, interacting in larger populations, form an important part of the architecture that enables our brain to perform the various functions required for cognition. Lastly, in the discussion section I address the relevance of the results, the compatibility of population coupling and phase-coding, the relevance of phase-coding in a proposed model for neuronal representations of conscious experience, and how correcting for behavioural correlates is a necessity in reading information correctly from the brain.

Nederlandse samenvatting

De hersenen van zoogdieren kunnen verbazingwekkende cognitieve functies uitvoeren. De berekeningen waarmee het brein deze functies uitvoert draaien op een netwerk van neuronen die met elkaar communiceren. De signalen van communicatie in dit netwerk kunnen worden beschreven als een neurale code, die door de neurowetenschap wordt benaderd via de verschillende, meetbare vormen van hersenactiviteit. In de neurofysiologie kunnen we de elektrische activiteit van groepen neuronen onderzoeken tijdens cognitieve processen in wakkere dieren, waarna we het gedrag van het dier met neuronale activiteit kunnen correleren.

In dit proefschrift onderzoeken we ten eerste de correlatie tussen het vuren van actiepotentialen van individuele neuronen en neuronale populaties (hoofdstuk 2). Deze correlatie kwantificeert de mate van koppeling van een neuron met de populatie-activiteit in een bepaald gebied. We bestuderen hoe neuronen aan populaties gekoppeld zijn binnen en tussen de visuele cortex, de snorhaarvelden van de somatosensorische cortex, de perirhinale cortex, en het CA1 veld van de hippocampus, in vrij bewegende ratten. We vinden verschillende niveaus van koppeling binnenin de verschillende gebieden, die overeenkomen met de fysiologische architectuur zoals we deze kennen uit andere studies, bijvoorbeeld over het bekende sterk synchrone vuurgedrag van de CA1 cellen. Daarnaast vinden we dat koppeling tussen de verschillende gebieden minder temporeel precies is in vergelijking met koppeling binnenin individuele gebieden, waarschijnlijk vanwege de polysynaptische routes die een signaal aflegt tussen gebieden. Koppelingen binnenin en tussen gebieden zijn over het algemeen positief gecorreleerd, vooral voor wat betreft de koppelingen van cellen ui het CA1 veld met een ander gebied (visuele cortex, somatosensorische cortex of perirhinale cortex). Daarnaast hebben we 'broadcasting' cellen kunnen identificeren, welke weinig koppeling met hun lokale populatie tonen, maar sterke koppeling met externe gebieden. Hierna plaatsen we de mate van koppeling in een cognitieve context. Ten eerste berekenen we de correlaties tussen de spatiële selectiviteit van cellen met de sterkte van hun koppeling, en vinden we een negatieve correlatie van deze selectiviteit met koppeling, noemenswaardig sterk binnen de CA1 regio. Dit schrijven we toe aan de tegenstelling tussen hoge mate van specificiteit in de informatie die nodig is voor de hoge ruimtelijke selectiviteit enerzijds, en het gebrek aan specificiteit van sterke populatie-koppeling. Ten tweede relateren we de koppeling aan de toestand van de hersenen zoals bij waken en slapen, en vinden we een afname in koppeling binnenin gebieden in non-REM slaap, maar instandhouding van de algemene koppelingsniveaus tussen de verschillende gebieden tijdens non-REM slaap, de rustige wakkere toestand, en actieve toestand: alleen tijdens non-REM slaap vinden we verminderde koppeling tussen CA1 cellen en de drie andere regio's.

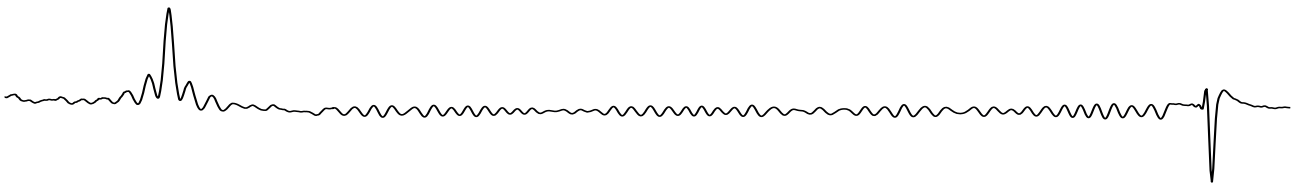
In hoofdstuk 3 onderzoeken we fase-codering als een relevante parameter in neurale codering. Tijdens een multisensorische detectietaak, uitgevoerd door muizen van wie de kop in positie wordt gehouden, onderzoeken we hoe de actiepotentialen van neuronen in de visuele cortex correleren met de fase van het theta ritme (~10 Hz) van het Locale Veld Potentiaal (LVP). We vinden dat een subpopulatie van fase-vergrendelde neuronen, die

reageren op de visuele en audiovisuele stimulatie, hun voorkeur van de fase-van-vuren ten opzichte van het LVP aanpassen tussen enkel visueel en audiovisuele condities. Daarnaast vinden we in een subset van cellen ook een verandering in de verdeling van fases van vuren afhankelijk van de oriëntatie van de visuele stimulus. Deze resultaten sluiten aan bij het theoretische model van Pennartz (2009), dat beschrijft hoe fase-codering kan fungeren als parameter voor relationele, multisensorische representaties tijdens perceptie, terwijl de representatie van de visuele prikkel stabiel blijft.

Ten slotte rapporteren we over een belangrijk concept in het interpreteren van neurale codering: de kennis van taak-irrelevante signalen in de data. Specifiek gezegd, zelfs in hoofd-gefixeerde muizen wordt motor-gerelateerde neuronale activiteit gevonden over de gehele neocortex. In onderzoek naar multisensorische integratie kunnen cross-modale sensorische signalen mogelijk 'vervuild' zijn met activiteit voortkomend uit motorisch gedrag. In hoofdstuk 4 correleren we orofaciale beweging van de muis met neuronale activiteit tijdens dezelfde multisensorische detectietaak als in hoofdstuk 3. We maken gebruik van een vooraf ingestelde vertraging in de gedragsrespons in de taak, en onderzoeken of dit uitstel wel of geen motor-gerelateerde activiteit bevat. De mate van spontane orofaciale beweging is laag tijdens de uitgestelde-respons periode, en nadat de muis een gedragsrespons genereert zien we een sterke stijging in motorische activiteit en gerelateerde actiepotentialen in V1 neuronen. Tijdens de uitgestelde-respons periode wekken sterke auditieve stimuli een orofaciale respons op, en gerelateerde neuronale activiteit in V1 neuronen. Echter, sterke of zwakke visuele stimuli induceren geen sterke motorische respons. Hoewel visueel selectieve neuronen ook correlaties met motor activiteit laten zien, hebben we een subpopulatie van visuele neuronen kunnen identificeren welke informatie over de stimulus in hun vuurgedrag coderen, zonder correlatie met orofaciaal gedrag.

De genoemde studies onderzoeken verschillende aspecten van neurale codering. De netwerken van neuronen die samenwerken in grotere populaties vormen een belangrijk deel van de architectuur waar ons brein verschillende cognitieve functies mee kan uitvoeren. In de afsluitende Discussie stel ik de relevantie van de resultaten aan de orde, de vergelijking tussen populatiekoppeling en fase-codering, de fase-codering in het voorgestelde model voor bewuste representaties in de hersenen, en hoe een analyse van gedragsgerelateerde correlaten noodzakelijk is voor het kunnen interpreteren van informatie gecodeerd in het brein.

Acknowledgements



By now, the benefit of gratitude is well known (Diniz et al., 2023) and as such, I would do myself a disservice if I did not take the time to be grateful for the people without whom this thesis would be – at the very least – severely lacking in interest.

Over the course of roughly 7 years you meet, work with, and receive support from many people. Some fade into the background over the years, some arrive on the scene at a later date, and some stay prominent in memory due to other factors than scientific collaboration. The people below have in some way been involved in the creation of this thesis, ranging from scientific collaboration to establishing a good social environment. Just like how a "simple" single neuron requires billions of partners to create our world, so too did I require all mentioned here to complete this thesis.

I am truly scared of not doing everyone justice, so at first: to anyone who feels even the slightest bit responsible for anything related to this thesis, thank you!

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I would like to thank my promotor and main supervisor, **Cyriel Pennartz**. Since my post-interview phone call, which ended with the confirmatory question (paraphrased): "[...] if you want to accept this position?", I am truly thankful for being trusted to work on this project. And, of course, the numerous discussions, advise and comments have been instrumental in completing the papers of this chapter.

My thanks go out to **Jeannette Lorteije.** You held my hand in the first years of the project as my daily co-supervisor, until you moved towards a new position in the IVD of the CDL at the Radboud University Nijmegen in 2020. I have learned a great deal in terms of animal science from you. As a fellow animal lover, I really appreciated the strict lessons on animal safety and welfare. The RUN is lucky to have you.

After Jeannexit 2020, **Conrado Bosman,** stepped in as the on-site co-promotor (Jeannette remaining co-promotor). I believe no other lab-members shared my passion and interest for music as much as you, but luckily you are also extremely well versed in advanced analysis on oscillations, which happened to coincide perfectly with my plans at the time. You know how I can never say no to a jam, so you can always give me a call if you need a percussionist (I'll bring my own brushes).

CSN group
Since 2017 I had the pleasure of sharing labs, successes, and frustrations with several amazing people in the CSN lab. I can legitimately say that I cannot think of a person who I didn't like having around for discussions, lunch, a drink or just the briefest of chats.

Several people have been noticeably crucial in the work presented here. First of all, I would like to thank **Medina Husic,** my first paranymph, and co-author of chapter 4. You are the perfect example of how science tends to draw out interesting people who are nothing but themselves. Besides the work on chapter 4, thanks for your magical ways to de-stress the lab. **Jeroen Bos**, impromptu technician, lab manager, senior-senior, and all-round chill dude.

Instrumental as the experimentalist who gathered the Touch and See dataset. I literally would not have been able to write chapter two without you. Thanks a lot, to my fellow PhD puppies, **Matthijs Oude Lohuis**, **Jean Pie**, and **Julien Fiorilli**, who started a bit before me. You just running ahead of me helped me a lot in learning the specific technicalities from the CSN lab. Besides, you were just amazing to have around, and laugh about why the hell we would have to translate complex multi-modal and -dimensional data to our simple human brains. Next, I had the pleasure of sharing my laboratory with **Roos (Rosanne) Tuip**. We tackled quite some technicalities in A4.24, and I'm happy I didn't have to do this alone. I wish you, Julien, and Elias all the best. **Thijs Ruikes**, technically a later generation of PhD students, although you even finished before me. Thanks for establishing the coffee ritual in the lab. Furthermore, your analytic prowess and our coinciding work on phase-coding was truly helpful (and fun). **Pietro Marchesi**, our analyst, seemingly able to magically conjure up advanced analysis in the blink of an eye. *Grazie mille* for your help on chapter 2, and other analysis queries. Still not sure if you were being paid to help, liked to code, or were just super friendly. **Judith Lim**, and **Paul Mertens**, thanks for the peanut butter as well as all the help. I couldn't imagine better office-neighbours. **Gerjan Huis in 't Veld,** our lab-manager / technician, you have been a helpful beacon in the lab throughout. **Mariel Müller, Jeroen van Daatselaar, Joao Patriota, Luca Montellisciani, Mathis Baßler, Eric Dijkema, Gerjan Huis in 't Veld, Guido Meijer, Laura van Bavelaar, Lillian Emming, Kengo Takahashi, Junying Wang, Andreas Franzke, Chris Jungerius, Sietse Kiewiet, Sabine Gnodde, Amber van Mierlo, Andreas Knobben, Lars Kopel:** thanks for all the shared ideas, and the amazing times together. I can't imagine anyone of you not making the place better by just being there. To my computational colleagues: we might have not worked together very directly, neurophysiologists can learn a lot from the amazing stuff you guys are doing. Thanks to **Rares Dorcioman, Parva Alavian, Matthias Brucklacher, Giulia Moreni** (don't underestimate how cool your stuff is to a physiologist), **Kwangjun Lee, Franscisco Pàscoa dos Santos, Abhirup Bandyopadhyay**.

We've had more PIs in our lab, besides my supervisors that always made their expertise available. **Umberto Olcese**, besides our close managerial relation, I was always able to sneak in a neuroscientific question or two (or a laugh). Thanks for your pragmatic and clever thoughts. **Jorge Mejias, Carien Lansink, Wim Ghijsen, Jan-Willem de Gee, Mototaka Suzuki, Jolien Francken:** You have all shared some of your expertise at one point or another, but more importantly also a smile and a laugh. Thank you!

Interns

I've had the pleasure of supervising three amazing MSc students during my PhD, who have all added significant value to this thesis. **Susanna Marques Mota Madeira Jorge**, I've learned supervising a lot from you as my first intern. Your heart for the welfare of the mice, and there for the precise and successful development of the behavioral task was great to see. **Jeroen Dijkmans,** together we have worked hard on dissecting various analysis, which I was still grateful for until the final stages of my own analysis. Good luck with your own PhD at the AUMC! **Felice Veen**, your enthusiasm was astounding and unexpected. From surgeries to coding, it either felt like fun or a challenge. Good luck with your own PhD at the NIN! Lastly, Thanks to Medina's student **Allegra Fagone** with the histology of my mice.

Supportive personnel
Many things in this thesis were not possible without the help from the support from the Technical Centre at the Faculty of Science, and specifically I want to call out **Tjeerd**, **Udo**, **Gerrit**, **Johan**, **Ronald**, and **Tristan**. From the Animal Facility SILS, a big thanks to animal caretaker **Chris Wijs**, and the Instantie Voor Dierenwelzijn **Rob** and **Miriam**. Next, **Aly**, and **Gideon** from the SILS management side, always available for administrative help and a friendly chat. Lastly, under the flag of the HBP we've had several managerial personnel in the lab with who I've had the pleasure of working (and traveling) with: **Yasmin Mzajek**, **Ingar Seeman** and **Hanna Bode**. In the same vein, **Angelica da Silva Lantyer**, whom I've had the pleasure of knowing since my time in Nijmegen, fulfilled a broad managerial role in the lab, but an even bigger role as empathetic, assertive figure. I've learned a lot from you and still continue to do so.

Other scientific personnel
Several collaborators have been of help with aspects of this thesis. **Martin Vinck** was, together with Jeroen Bos, the original father of the Touch and See dataset. **Michael Okun**, together with Cyriel Pennartz, conceived of the original plan of the Population Coupling project. For 3D reconstructions of the recording sites of the rat brain, thanks to **Jan Bjaalie** and **Ingrid Reiten** from University of Oslo. Lastly, I had the pleasure of being funded and working within many amazing people in the Human Brain Project.

PhD commission
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Friends
Besides a thriving scientific community, I'm extremely grateful for several groups of friends who have either actively helped me in some ways or were one of the essential cogs in the complex social machine. My spectrally interesting friends from the south (in the order of the WhatsApp group): **Dennis, Fersy, Gerarda, Juul** (thanks for keeping track of the years), **Loes, Luuk, Marieke, Marly, Melissa, Peter** (seriously, going out into nature for multiple days is an underrated anti-stress hack), **Roel, Roomana, Shiro, Tess, Thom, TJ, Tom, Wout and Wouter S** . I came to realize it's rather unusual to still keep track of a group of friends for so long (I think I've known Tom and Juul for 21 years now?). After a while, the arbitrary line on the scale of importance between friends and family blurs a lot, and I'm happy it does.

Next, since moving to Ede I luckily had the pleasure of getting involved in a thriving sub-community of fellow biologists, counter-culturalists and musicians: **Twan** and **Chantal** (good to have someone still being legitimately trying to understand my scientific ramblings at 02:00 0' clock), **Xander** and **Elyse**, **Luigi, Bas** and **Eelke**, and the bouldering/Peppel crew. Similarly, thanks to the entire team of Astrantionauts.

Furthermore, anyone who knows me a little bit knows that music is an extremely important part of my life, not only in listening, not only in creating, but also the vibrant community and friends I have made here. I am very grateful so share my anger and angst with my friends from Canyon Literature, **Wouter v E, Max, Oskar, Glenn** and **Donny.** You guys probably underestimate how good it has been for my psyche to join the band. Additional shout out to **Roger** and **Ramon**. I would also like to call out the various bands, communities and members of the music community who helped me in using music as the amazing creative outlet it is: Demoralizer, A Part of the Problem, DEEPROOT, Conquer All, the Core-munity and the Astrant musician/Sterrenstof-community. A special mention to DEEPROOT's graphical artist **Anna Molly** for designing the cover.

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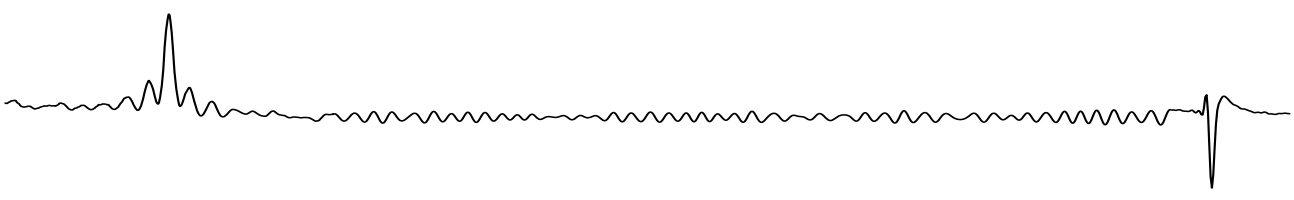
Next, I would like to bestow thanks on my family. My parents (**Maaike Blom** and **Gerrit Jan Dorman**) for supporting me in everything I do, as far as I know. In fact, I believe without your upbringing I would have not be able to unfold as a person not afraid to ask questions and follow the passion of knowing more about the world. My brother and sister, **Jorrit** and **Marije Dorman**, who (I think) share a similar neurological design with me leading to a similar passion for learning new things. In addition, thanks for Marije's husband **Jochem v/d Hoven** for picking up the guitar. Additionally, I want to specifically thank my aunts **Pia Overgaag** and **Ypie Blom** for providing me with a bed during necessary moments, and finish with thanking my entire family for being the welcome and friendly people as I've come to know them.

I have the pleasure to share my daily life with the most amazing creatures which never fail to brighten the worst of days: **Fira, Tamago, Stip Meowrits**, and yes, even **Cedy**. Either you have infected me with *Toxoplasma gondii* to abnormal levels, or cats truly carry a spark of the divine.

Of course, I want to thank my second paranymph, wife, girlfriend, and beautiful girl **Minty Vissers** for her entire existence with me. I can't imagine anyone else I want to share all my pain and pleasure with. Please remember I will always want you by my side, but life tends to have opinions of it's own. Nevertheless, you know I will always get back to you.

Laboratory animals
Lastly, I wanted to extend my thanks to the animals that have been subjected to my research. There is a very fine ethical line between the benefits of *in vivo* neuroscientific research and respecting and caring for nature and its inhabitants. In my opinion, is not yet possible to learn the fundamental mechanisms about the brain without looking in actual organisms. We as researchers have the obligation to be as efficient as possible with the information that we can gather from these animals, and to be forever grateful.

Statistical glossary



Akaike Information Criterion	Estimator for quality of a statistical model given a set of data. Based on information theory, it estimated the relative amount of information list by a given model. The less information is lost, the higher quality the model is.
ANOVA	Analysis of variations, a statical test for compare the means of two or more groups. Variance of the mean within and between groups are compared. The comparison is done via an F-test. Assumes independent samples, normal distribution and homoscedasticity.
Bayesian Information Criterion	Estimator for quality of a statistical model given a set of data, based on a penalization of the amount of parameters on the outcome of the Maximum Likelihood Estimation
Benjamini - Hochberg procedure	A method to calculate the False Discovery Rate. It adjusts a threshold of significance based on the ranks of all p-values, amount of tests, and the choses false discovery rate (generally 0.05). Generally aimed to be less conservative than the Bonferroni correction, and suitable for independent and dependent (though not universally) datasets.
Binomial distribution	A probability distribution resulting from a binary question (i.e. true or false) with probability p for y=true, for n amount of samples. Given a certain probability of true this distribution would center around n*p.
Binomial Generalized Linear Model	A regression model which models the probability of "success", generally applied to a binary question (true or false; stimulus selective units versus no stimulus selective units). The probability of success, or the response Y, would be modelled following a binomial distribution. A GLM has a set of predictors on which it tries to model the outcome (such as trial type, recording session, neuron ID, animal ID). A Link Function is applied on the linear combination of the predictors to the outcome Y. Binomial GLMs are suitable for testing true or false, or A or B questions, and could take a wide range of predictors into account.
Bonferroni correction	A method of multiple comparison correction, adjusting the p-value of a number of statistical tests based on the amount of tests by dividing the current threshold by the amount of tests under the same hypothesis. A conservative correction, prone to increased Type II errors.
Chi-squared test for independence	A test for the effects of categorical variables on a test-statistic. Generally visualized in the shape of a 2x2 contingency table Specifically, the Chi-squared test (or $\chi 2$ test), assumes a Chi-squared distribution under the null hypothesis, which would if the observations were all independent. Requires > 5 independent samples.

Circular MANOVA	MANOVA adjusted for circular data. In essence MANOVA performed on sine and cosine of an angular dataset. Assumes independent samples, normal distribution of transformed data
Circular-linear correlation	A correlation method adapted to compare linear and circular datasets, such as comparing phase-of-firing with firing rates.
Clustering	Any type of algorithm which takes an N-dimensional dataset and tries to identify which points in the dataset would "belong together" in a same cluster.
DBSCAN clustering method	Density-Based Spatial Clustering of Applications with Noise (DBSCAN) is a clustering algorithm. It is non-parametric, leaves out noise clusters and does not require a pre-determined set amount of clusters it should look for. It requires parameters set for the radius to search for neighboring points, and an amount of minimum points per cluster.
False Discovery Rate	A multiple comparison correction method to assess the rate of Type I errors by multiple comparisons. Various procedures exist to calculate the FDR.
Freedman-Diaconis method	A method to select the width of bins of histograms from a continuous dataset. The aim is to balance variation in the underlying distribution to make a visually accurate histograms. Makes use oft the interquartile range (*IQR*) as opposed to the standard deviation, making it less susceptible to outliers.
Friedman test	Non-parametric alternative to the repeated measures ANOVA. Based on rank. Assumes independent samples within groups.
F-test	A test comparing variances. Used as post-hoc test to the ANOVA. Assumes independent samples, normality and homoscedasticity.
Gaussian Distribution	See Normal Distribution
Generalized Linear Mixed Model	Statistical model of extended linear regression combining Generalized Linear Models and Mixed Models, providing a means to test an outcome with both fixed and random effects. Said model is trained to fit the data based on the effects and can test the significance of any of the predictors provided. Generally used for non-normally distributed, dependent datasets. Ideally suitable with hierarchical or grouped datasets, such as neurons within sessions within animals. NOTE: fit for repeated measures and count data (as opposed to continuous and nomila.

Kolmogorov-smirnov goodness of fit test	Non-parametric test of equality, able to test if a dataset comes from a given reference probability distribution, such as a normal distribution.
Kruskal-Wallis test	Non-parametric equivalent of the ANOVA. Tests if group distributions differ significantly. Based on ranks. Assumes independent samples, with distributions of similar shapes.
Laplace approximation	A method to approximate complex probability distributions, generally with normal distributions. Used to make certain statistical problems with complex models more efficiently computable.
Link function	A function between expressions of a model and the outcome. In the context of Linear Models, this often takes the form of a logit function on the linear expression of the model.
MANOVA	Multivariate analysis of variation, a statistical test for comparing multivariate sample means. An alternative to analysis of variance (ANOVA) testing for multiple dependent variables. Assumes independent samples, normality and homogeneity of covariance.
Maximum Likelihood Estimation	A method to estimate the parameters of a probability distribution or statistical model to best fit the observed data. This is done by maximizing a chosen likelihood function under the observed data.
McNemar test	Statistical test on paired nominal data. Applied to dichotomous data, i.e. comparing A=true or false with B=true of false, generally in the shape of a 2x2 contingency table. Generally performed on comparison two tests being either positive or negative, by comparing if the various combinations of outcomes of the two tests are equal (or homogeneous).
Multiple comparison correction	A set of methods to control for family-wise error rates or false discovery rates when performing multiple hypothesis testing. When applying multiple statistical tests with a certain threshold, the risk of a result crossing said threshold by chance instead of the actual hypothesized effect increases. Thus, methods have been devised to correct results of statistical tests for such multiple comparisons. Generally, such tests are applied on tests of the same hypothesis in a dataset, and adjust the resulting p-value based on the amount of tests performed. Different tests have different effects, such as increases in Type I or Type II errors.

Normal distribution	Also known as a normal distribution, a typical distribution generally assumed to be a normal, non-skewed distribution. Often assumed in natural sciences to represent unknown distributions (Based on Central Limit Theorem). Based on mean and variance in the data as: $$y = \frac{1}{\sigma\sqrt{2\pi}} e^{-\frac{(x-\mu)^2}{2\sigma^2}}$$
Normality	Assuming a normal distribution.
Null Distribution	Null distribution is the distribution of the data if there were no effects of any hypothesized variables.
Pearson Correlation	A measure of linear correlation between two datasets. Assumes normality and homoscedasticity.
Permutation test	Collective name for any type of statistical test which is performed numerous times, generally with shuffling the underlying dataset to compare the actual test statistic with a shuffled distribution. Non-parametric and free of assumptions, and dependent on the type of approach able to retain certain aspects of the dataset (i.e. for instance, shuffling short term temporal correlations while retaining global correlations).
Permutation-based clustered test	A test for finding significant clusters of the data in a continuous dataset. Suitable to detect significant differences in certain parts of continuous dependent variable which can have significant effects between two groups. Works by finding significant points across all dependent variables with a predetermined test, constructing a cluster from adjacent significant points. The test statistics of such a cluster is compared with a null-distribution based on shuffling relevant labels within the dataset, computing the test-statistics, construct clusters, and compute cluster-level statistics. Suitable for data which may have a relation along the dependent variables, such as temporal, spatial or frequency relations (i.e. time-bins close to one another might be affected in a similar way by the same cause). Requires exchangeability of shuffled parameter under the null hypothesis
Poisson Pseudo-R2	A measure of model quality, specifically Random Forests. Generally quantified as a difference between observation and prediction from a model. The Poisson distribution is assumed as the underlying distribution for the data.
Rayleigh test	A test for circular uniformity.

Repeated measures ANOVA	ANOVA applied on datasets with repeated measures, i.e. under multiple measurements of the same variable under different conditions. For instance, LFP power in the same animals along different frequencies.
Schreier-Ray-Hare test	Non-parametric alternative to a two-way ANOVA, an extension of Kruskal-Wallis test for two or more factors. Tests based on ranks. Assumes independent samples, with distributions of similar shapes.
Shuffling procedure	Shuffling a metric or parts of the data. Generally, this is done to create a empirically based null-distribution. Shuffling can be applied on labels (such as cell-type labels), or along time (such as randomly shifting the time, or randomly shifting pre-defined time bins). Dependent on the type of shuffle, this is generally aimed to remove any correlations in the dataset and assess the significance of the true measurement. Often combined with other statistical tests. Requires exchangeability of shuffled parameter under the null hypothesis
Spearman rank correlation	Non-parametric equivalent of the Pearson Correlation, based on rank.
T-test	Parametric test which assesses if two datasets overlap significantly under the assumption of student's T-distribution as the null hypothesis. Typically applied to test two normally distributed datasets. Can be applied on independent, or in the case of the paired t-test, paired data.
Type I error	A false positive. A statistical test indicating an observed effect is due to the hypothesized cause while it is in fact due to chance.
Type II error	A false negative. As statistical test indicating an observed effect is due to random chance while it is in fact due to the hypothesized cause.
Wald test	A test for significance of the parameters of a fitted model such as a Generalized Linear Models. Used as a post-hoc test to test compare specific combinations of parameters. Specifically, the Wald test of estimated marginal means tests differences among adjusted group means from a model.
Watson U2 test	Non-parametric statistical test for comparing two distributions of circular data. Null hypothesis states the two distributions are the same. Based on ranks. Assumes independent samples.

Wilcoxon Rank-sum test	Non-parametric equivalent of the T-test. Tests the null hypothesis that two independent datasets are from the same distribution, based on the ranks of the data. Assumes independent samples, within distributions of similar shapes. Also known as Mann-Whitney test.
Wilcoxon Signed-rank test	Equivalent of the Wilcoxon Rank-sum test but for paired data (i.e. dependent).
Z-scoring	Method of normalization. Standardizing a dataset by a mean and standard deviation of it's own or a certain baseline dataset. E.g. normalizing firing rate responses to a stimulus versus a baseline period; or normalizing a metric versus a shuffled distribution.

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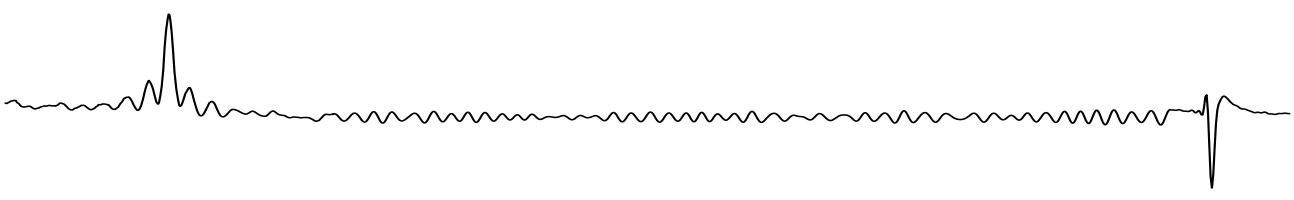

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Universiteit van Amsterdam
Faculteit der Natuurwetenschappen,
Wiskunde en Informatica