



THE UNIVERSITY *of* EDINBURGH

Edinburgh Research Explorer

A sensorimotor account of visual attention in natural behaviour

Citation for published version:

Schumann, F 2012, 'A sensorimotor account of visual attention in natural behaviour', University of Osnabrück.

Link:

[Link to publication record in Edinburgh Research Explorer](#)

Document Version:

Publisher's PDF, also known as Version of record

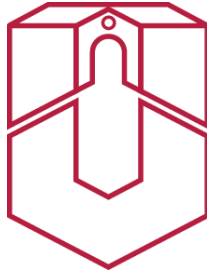
General rights

Copyright for the publications made accessible via the Edinburgh Research Explorer is retained by the author(s) and / or other copyright owners and it is a condition of accessing these publications that users recognise and abide by the legal requirements associated with these rights.

Take down policy

The University of Edinburgh has made every reasonable effort to ensure that Edinburgh Research Explorer content complies with UK legislation. If you believe that the public display of this file breaches copyright please contact openaccess@ed.ac.uk providing details, and we will remove access to the work immediately and investigate your claim.





A Sensorimotor Account of Visual Attention in Natural Behaviour

Dissertation
zur Erlangung des Grades
”**Doktor der Naturwissenschaft**“
im Fachbereich Humanwissenschaften
der Universität Osnabrück

vorgelegt von

Frank Schumann

Osnabrück, im Mai 2012

Gutachter:
Prof. Dr. Peter König (Osnabrück)
Prof. Dr. Wolfgang Einhäuser (Marburg)
Prof. Dr. Erich Schneider (München)

Abstract

The real-world sensorimotor paradigm is based on the premise that sufficient ecological complexity is a prerequisite for inducing naturally relevant sensorimotor relations in the experimental context. The aim of this thesis is to embed visual attention research within the real-world sensorimotor paradigm using an innovative mobile gaze-tracking system (EyeSeeCam, Schneider et al., 2009).

Common laboratory set-ups in the field of attention research fail to create natural two-way interaction between observer and situation because they deliver pre-selected stimuli and human observer is essentially neutral or passive. EyeSeeCam, by contrast, permits an experimental design whereby the observer freely and spontaneously engages in real-world situations. By aligning a video camera in real time to the movements of the eyes, the system directly measures the observer's perspective in a video recording and thus allows us to study vision in the context of authentic human behaviour, namely as resulting from past actions and as originating future actions.

The results of this thesis demonstrate that

- (1) humans, when freely exploring natural environments, prefer directing their attention to local structural features of the world,
- (2) eyes, head and body perform distinct functions throughout this process, and
- (3) coordinated eye and head movements do not fully stabilize but rather continuously adjust the retinal image also during periods of quasi-stable "fixation".

These findings validate and extend the common laboratory concept of feature salience within whole-body sensorimotor actions outside the laboratory. Head and body movements roughly orient gaze, potentially driven by early stages of processing. The eyes then fine-tune the direction of gaze, potentially during higher-level stages of visual-spatial behaviour (Studies 1 and 2).

Additional head-centred recordings reveal distinctive spatial biases both in the visual stimulation and the spatial allocation of gaze generated in a particular real-world situation. These spatial structures may result both from the environment and form the idiosyncrasies of the natural behaviour afforded by the situation. By contrast, when the head-centred videos are re-played as stimuli in the laboratory, gaze directions reveal a bias towards the centre of the screen. This "central bias" is likely a consequence of the laboratory set-up with its limitation to eye-in-head movements and its restricted screen (Study 3).

Temporal analysis of natural visual behaviour reveals frequent synergistic interactions of eye and head that direct rather than stabilize gaze in the quasi-stable eye movement periods following saccades, leading to rich temporal dynamics of real-world retinal input (Study 4) typically not addressed in laboratory studies. Direct comparison to earlier data with respect to the visual system of cats (CatCam), frequently taken as proxy for human vision, shows that stabilizing eye movements play an even less dominant role in the natural behaviour of cats. This highlights the importance of realistic temporal dynamics of vision for models and experiments (Study 5).

The approach and findings presented in this thesis demonstrate the need for and feasibility of real-world research on visual attention. Real-world paradigms permit the identification of relevant features triggered in the natural interplay between internal-physiological and external-situational sensorimotor factors. Realistic spatial and temporal characteristics of eye, head and body interactions are essential qualitative properties of reliable sensorimotor models of attention but difficult to obtain under laboratory conditions. Taken together, the data and theory presented in this thesis suggest that visual attention does not represent a pre-processing stage of object recognition but rather is an integral component of embodied action in the real world.

Curriculum Vitae

Frank Schumann

Wiesenbachstraße 2a, 49080 Osnabrück, Germany, fschuman@uos.de
Born 11.02.1977, Bad Dürkheim, Germany

Journal Publications¹

Quantifying the Contribution of High- and Low-level Information to Active Vision: Top-down is the dominant mode under normal viewing conditions². Onat S., Açık A., Schumann, F., König, P. (in preparation).

*Eye-head coordination during free exploration in human and cat³. Einhäuser, W., Moeller, G. U., Schumann, F., Conrath, J., Vockeroth, J., Bartl, K., et al. (2009) *Annals of the New York Academy of Sciences*, 1164, p. 353-366

*Distinct roles for eye and head movements in selecting salient image parts during natural exploration⁴. Einhäuser, W., Schumann, F., Vockeroth, J., Bartl, K., Cerf, M., Harel, J., et al. (2009) *Annals of the New York Academy of Sciences*, 1164, p. 188-193

*Gaze allocation in natural stimuli: Comparing free exploration to head-fixed viewing conditions⁵. Marius 't Hart, B., Vockeroth, J., Schumann, F., Bartl, K., Schneider, E., König, P., et al. (2009) *Visual Cognition*, 17(6), p. 1132-1158

Effects of luminance contrast and its modifications on fixation behavior during free viewing of images from different categories⁶. Açık, A., Onat, S., Schumann, F., Einhäuser, W., & König, P. (2009) *Vision Research*, 49(12), p. 1541-1553

*Salient features in gaze-aligned recordings of human visual input during free exploration of natural environments⁷. Schumann, F., Einhäuser-Treyer, W., Vockeroth, J., Bartl, K., Schneider, E., & König, P. (2008) *Journal of Vision*, 8(14):12, p. 1-17

¹ Publications referred to in this thesis are marked with an asterisk.

² Contribution: provided methods and code for data analysis from Masters' thesis, data recording.

³ Contribution: data recording, manuscript

⁴ Contribution: experimental design, provided methods for analysis, interpretation, data recording, manuscript

⁵ Contribution: data recording

⁶ Contribution: provided methods and code for data analysis, manuscript.

*Human eye-head co-ordination in natural exploration⁸. Einhäuser, W., Schumann, F., Bardins, S., Bartl, K., Böning, G., Schneider, E., et al. (2007) *Network: Computation in Neural Systems*, 18(3), p. 267-297

Reports

Integration of Different Features in Guiding Eye-Movements. Schumann, F. (2010). Publications of the Institute of Cognitive Science, University of Osnabrück, Volume 11. (Master Thesis).

MINI: Mechanisms In Neuropsychological Issues. Albert, F., Griego J., James S., Kabisch C., Kolomiyets O., Kreitz U., Kunkemöller J., Liu J., Mühl C, Nagel S., Neubauer S., Schumann F. (2005). Publications of the Institute of Cognitive Science, University of Osnabrück, Volume 9.

Embodied cognitive science: is it part of cognitive science? Analysis within a philosophy of science background. Schumann, F. (2004). Publications of the Institute of Cognitive Science, University of Osnabrück, Volume 3, (Bachelor Thesis).

Invited Talks and Demonstrations

Schumann, F. & Ebert, M. (2010) “Optimal Sensory Integration of the feelSpace belt?”, Multisensory Perception and Action Group (Dr. Marc Ernst), MPI for Biological Cybernetics, Tübingen, 27.09.2010

Schumann, F. (2009) “Beyond Sensory Substitution: Learning the Sixth Sense”, Department of Systems Neuroscience, UKE Hamburg, 1.10.2009

Schumann, F. & Ebert, M. (2009) Demo of the feelSpace belt at the Workshop “Key Issues in Sensory Augmentation”, University of Sussex, Brighton, UK, 26-27.03.2009.

⁷ Contribution: experimental idea, data recording, data analysis & interpretation, manuscript.

⁸ Contribution: experimental design, data recording, manuscript.

Poster

König, S.U., Brunsch, V., Ebert, M., Fleck, S., Gameiro, R., Gasse, S., Goeke, C., Hanke-Uhe, M., Kaspar, K., Keyser, J., Krause, C., Lytochkin, A., Muil, R., Numonov, A., Sieveritz, B., Schmitz, M., Wache, S., Nagel, S.K., Schumann, F., Meilinger, T., Bülhoff, H., Wolbers, T., Büchel, C., König, P. (accepted): Properties and mechanisms of sensory enhancement, Spatial Cognition 2012, Kloster Seeon, 31.08.-03.09.2012

Ebert, M., Fleck, S., Goeke, C., Kaspar, K., Keyser, J., König, S., Krause, C.D., Muil, Nagel, S.K. Schumann, F., König, P. (2011). FeelSpace: A holistic study of sensorimotor contingencies. Banff Annual Seminar in Cognitive Science.

Kugler, G., 't Hart B.M., Kohlbecher, S., Bartl, K.; Schumann, F., König, P., Einhäuser, W., Brandt, T., Schneider, E. (2011): Deuteranomaly in natural visual search. Society for Neuroscience Meeting (SfN), Washington, USA, 12.-16.11.2011

't Hart, B.M., Kugler, G., Bartl, K., Kohlbecher, S., Schumann, F., Brandt, T., König, P., Einhäuser, W., Schneider, E. (2011): Real-world search strategies with normal and deficient color-vision, 34th European Conference on Visual Perception, Toulouse, France, 28.8. 1.09.2011

Kugler, G., 't Hart, B.M., Kohlbecher, S., Bartl, K., Schumann, F., Einhäuser, W., Brandt, T., Schneider, E. (2011): Eye Movements in the real world during visual search for colored candies, Basic and clinical oculomotor research – A tribute to John Leigh, Puerto Madera, Argentina, 25–27.3.2011.

Kugler, G., 't Hart, B.M., Bartl, K., Kohlbecher, S., Schumann, F., Einhäuser, F., Brandt, T., Schneider, E. (2011) Looking for Candy: Real World, feature based search, 9th Meeting of the German Neuroscience Society, Göttingen, 23-27.03.2011.

Kugler, G., 't Hart, B.M., Kohlbecher, S., Schumann, F., Einhäuser, W., Brandt, T., Schneider, E. (2011): Farb- und formbasierte visuelle Suche bei unterschiedlichen Farbsehfähigkeiten in natürlicher Umgebung, 55. Jahrestagung der DGKN, Münster, 16-19.3.2011.

't Hart, B.M., Vockeroth, J., Schumann, F., Bartl, K., Schneider, E., König, P. and Einhäuser, W. (2009). Gaze allocation during natural behavior in the real world, 8th Göttingen Meeting of the German Neuroscience Society

Schumann, F., Cerf, M., Harel, J., Vockeroth, J., Bartl, K., Schneider, E., König, P., Einhäuser, W. (2008). Eye- and Head Movements during Natural Exploration, Basic and Clinical Aspects of Vertigo and Dizziness, Kloster Seeon, 22.-25.6.2008

Schumann, F., Einhäuser, W., Vockeroth, J., Bartl, K., Schneider, E., König, P (2008). „Gaze-aligned tracking of human visual input during free exploration of natural environments“, Computational Vision and Neuroscience Symposium, Max Planck Institute for Biological Cybernetics Tübingen, 7-8.4.2008

Schumann, F., Einhäuser, W., Bardins, S., Bartl, K., Böning, K., Schneider, E., König, P (2007). Human gaze control in natural exploration, ESF Symposium “Three dimensional sensory and motor space: perceptual consequences of motor action”, Sant Feliu de Guixol, 6.-11.10.2007

Schumann, F., Acik, A., Onat, S., König, P. (2007). Integration of different features in guiding eye- movements, Proceedings of the 7th Meeting of the German Neuroscience Society, Göttingen.

Schumann, F. (2007). Embodied Cognitive Science: part of cognitive science? Analysis within Lakatonian Philosophy of Science, Interdisciplinary College 2007 of the German Computer Science Society, Focus Theme: Embodiment, Günne

Schumann, F., Acik A., Onat S., König P. (2006). Interaction of different features in guidance of eye- movements, Dynamics of Visual Perception Workshop at the Westf. Wilhelms-Universität Münster.

Schumann, F., Griego, J., James, S., Kunkemöller, J., Kabisch, C., Kolomiyets, A., Kreitz, U., Liu, J., Mühl, C., Nagel, S.K., Neubauer, N. (2004). Automatic affective processing: Priming effects on the perception of affective valence in visual stimuli, Symposium “Perspective in Cognitive Science”, Osnabrück.

Land, R., Schumann, F., Scholz, J., Helduser, C., Carl, C., Schindler, S., Corves, C., Lesemann, E., Herzog, M. (2003). Ultra-Fast Object Segmentation, Proceedings of EuroCogSci '03, Osnabrück.

Proposals Drafted

Grant proposal feelSpace (“Sensory enhancement – learning a new sense”), Deutsche Forschungsgemeinschaft⁹

Ethics proposal feelSpace, University of Osnabrück, Deutsche Gesellschaft für Psychologie

⁹ Contribution: Final draft of manuscript, except for section 2.2 (Eigene Vorarbeiten) by Peter König. Section on behavioral methods drafted with Robert Martin, section on Sleep EEG drafted by Saskia Nagel and adapted by myself.

Thesis and Study Projects Supervised

Modulation of spatial perception in a congenitally blind subject by means of a vibrotactile direction signal. Bachelor thesis of Anna-Antonia Pape

Preparations to study the neural correlates of a vibrotactile sensory augmentation device: Implementation of an fMRI path integration experiment and development of an MR-compatible feelSpace belt. Bachelor thesis of Johannes Keyser

feelSpace behavioural tests: Navigation performance and multimodal integration, Master study project of Manuel Ebert and Robert Muil

Student Research Assistants Supervised

feelSpace psychophysics: Manuel Ebert

feelSpace homing: Carina Krause

feelSpace nystagmography: Caspar Goecke, Bastian Schledde

feelSpace fMRI: Johannes Keyser

feelSpace embedded software- and electronics miniaturization: Robert Muil

feelSpace belt mass-construction: Caspar Goecke, Jan Herding, Meike Rugenstein, Bastian Schledde, Maria Schmitz, Martina Lau, Antje Starch, Matthias Hampel

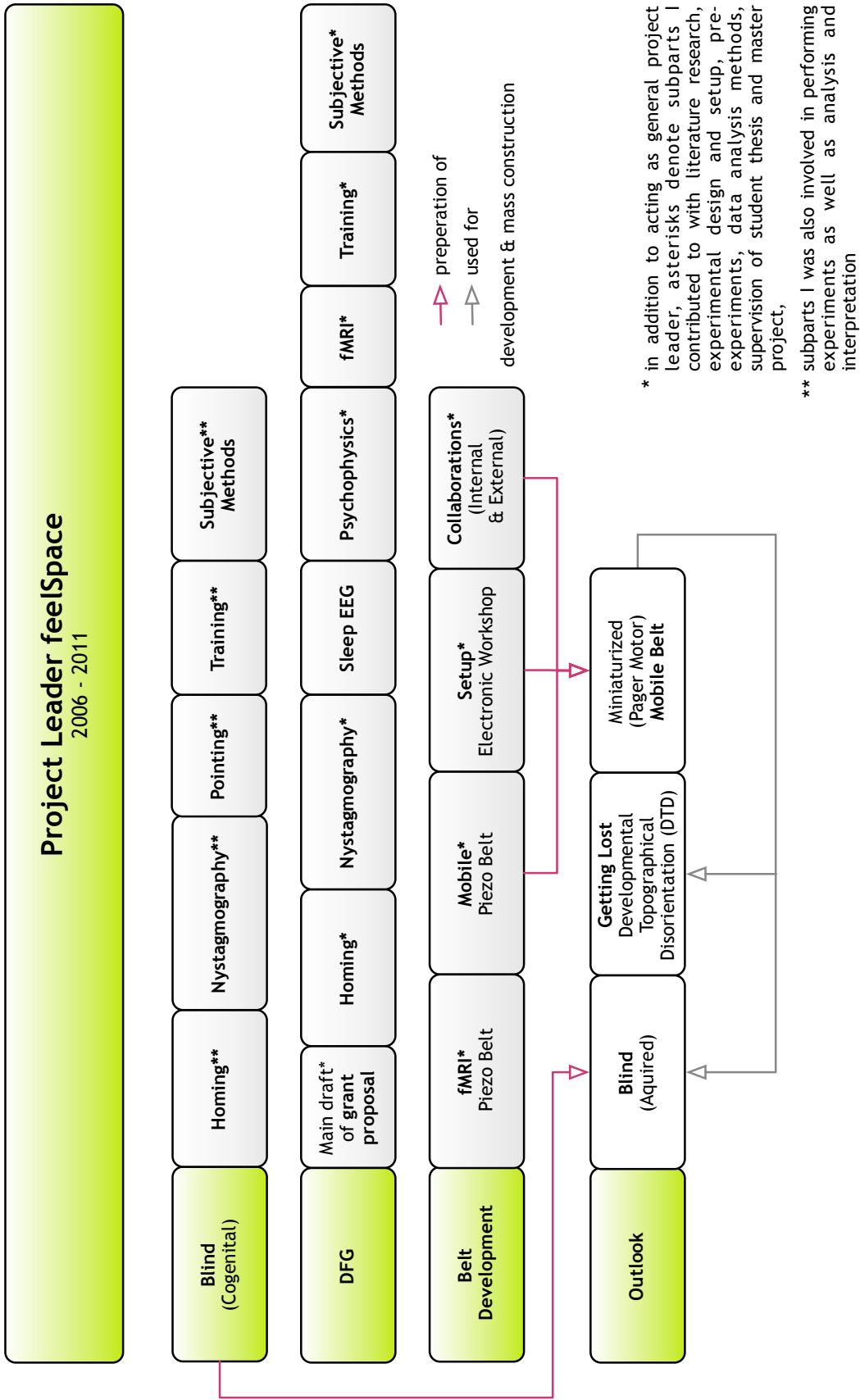


Figure 1-1: Contribution to the feelSpace project.

Education

- 10/2006 - **PhD candidate** with Prof. Dr. Peter König, *Department of Neurobiopsychology, Institute of Cognitive Science, University of Osnabrück, Germany.*
- Project feelSpace:**
- Project leader
 - Sensory enhancement with vibro-tactile information about magnetic north supplied by a haptic compass belt
 - Supervision of up to 11 research assistants
- Project EyeSeeCam:**
- Eye-tracking and visual attention during spontaneous behaviour in real-world environments
- 2002-2006 **Master of Science in Cognitive Science** (with distinction), *University of Osnabrück, Germany.*
- Master-Thesis: ‘Integration of different features in guiding eye-movements’ in the Neurobiopsychology Lab of Prof. Peter König, using Bayesian and information theoretic data analysis methods, Grade A (Excellent, 1.0).
 - Independent research project on eye-tracking in real-world environments (EyeSeeCam)
 - Study project on the impairment of cognitive functions in patients with brain lesions in cooperation with Prof. Dr. F. Albert, neurosurgeon at the local Paracelsus clinic. Supervision: Dr. Jaqueline Griego.
- 10/2001 - **Visiting Student**, *University of Warwick, Coventry, UK,*
03/2002 *Departments of Psychology and Philosophy*
- 1999-2002 **Bachelor of Science in Cognitive Science** (with distinction), *University of Osnabrück, Germany.*
- Thesis: “Embodied cognitive science: is it part of cognitive science? Analysis within a philosophy of science perspective”, Supervisor: Dr. Ian E. Morley, University of Warwick, UK, Grade A (Excellent, 1.0)
- 1996-1999 **Jazz Piano Programme**, *Frankfurter Musikwerkstatt (state approved school of Jazz and Popular music), Frankfurt, Germany.*
- WS 1996/97 **Magister programme in philosophy and musicology**
- WS1997/98 *University of Heidelberg, Germany*
- 1993-1996 **Abitur**, *Technisches Gymnasium Ludwigshafen am Rhein, Germany*

1 Acknowledgements

This thesis rests on the generous help of many. Foremost, I thank my supervisor Peter König for organizing his lab as a space of excellence, encouragement and freedom where people can grow in an inspiring project-based learning atmosphere. I also thank Wolfgang Einhäuser for working so intensely together, I have learned a lot from you.

Many thanks also go to my office mates, for your thoughts and the fun, your expertise, your open ears, for the “conference calls”, and your willingness to share: Robert Martin, Daniel Weiller, Nora Nortmann, Johannes Keyser, Hannah Knepper, Niklas Wilming, Thorsten Betz, Stephan Geuter, Selim Onat, Alper Acik, Tim Kitzmann, Cornell Schreiber, Manuel Ebert, Robert Muil; and of course everyone else in the NBP crowd, a very special group. Many more people would need to be mentioned from Osnabrück CogSci, more than I can list.

I am indebted to those reviewing my dissertation: Christa Deiwiks, Mike Beaton, Tom Froese, Frank Jäkel, Jan Peters, Marek McGann, Miriam Kyselo, Nora Nortmann, Marius t’Hart, Steve Torrance, and in particular Nicolas Neubauer and Christian Artmann for the linguistic surgery of the abstract.

1.1 feelSpace

My PhD work has turned into an intense exercise in project management, supervision and teamwork. During my work as project leader of feelSpace (DFG Erweitertes Sensorium - Lernen eines neuen Sinnes (KO 3359/4-1)), many thanks for the fruitful cooperation and discussions go to:

- **Functional Magnetic Resonance Imaging (fMRI):**
Dr. Jürgen Finsterbusch, Dr. Jan Peters & Prof. Christian Büchel (Institut für Systemische Neurowissenschaften, UKE Hamburg), Dr. Thomas Wolbers (Center for Cognitive and Neural Systems, University of Edinburgh)
- **Psychophysics:**
Dr. Tobias Meillinger (Department Prof. Bülthoff, Max-Planck-Institute for Biological Cybernetics, Tübingen)
- **Nystagmography:**
Dr. med. habil. Christian Schmidt (HNO Praxis Osnabrück), Dr. med. Thorsten Zehlicke (Universität der Bundeswehr, Hamburg)
- **feelSpace Blind:**
Dipl. Psych. Anna Best & Prof. Brigitte Röder (University of Hamburg)
- **Electronic Development for MRI and Wearable Belt Miniaturization:**

Uwe Klaas, Dipl.-Phys. Dirk Rathmann, Dieter Sobieralski & Werner Schniederberend
(Werkstatt für Elektronik und Informationstechnik, Universität Osnabrück)

- **Mechanical Development of Piezo Housings and Wearable Belt Miniaturization:**
Holger Heine & Uwe Kling (Feinmechanische Werkstatt, Universität Osnabrück)
- **Consultancy on fMRI Actuation Methods:**
Dipl.-Chem. Frank Baumgart (mr:confon GmbH, Kommunikations- und Antischallsysteme für die Kernspinttomographie, Magdeburg), Dipl.-Ing. Thomas Villgratner (Technische Universität München)
- **Electrical Insulation of Vibrating Piezo Actuators:**
Michael Suwe (ELANTAS Beck Electrical Insulation, Hamburg), Michael Müller (Conformal Coating GmbH, Esche), Uwe Reinink (UN Gerätebau, Entwicklung und Betrieb von Prüfgeräten, Osnabrück)
- **High-Voltage Security:**
Roswitha Zucht (Arbeitsschutz- und Gefahrstoffmanagement, Universität Osnabrück),
Valentin Haug (BueroVeritas, Zertifizierungsstelle für Medizingeräte, Türkheim)

1.2 EyeSeeCam

Within the EyeSeeCam project, my thanks go to my co-authors:

- Prof. Dr. Wolfgang Einhäuser & Dipl.-Psy. Marius t'Hart (Neurophysik, Universität Marburg)
- Prof. Dr. Erich Schneider, Dipl.-Inf. Johannes Vockeroth, Dipl.-Ing. Klaus Bartl, Dipl.-Inf. Stanislavs Bardins, Dipl.-Biol. Guido Böning, Dipl.-Inf. Stefan Kohlbecher (Zentrum für Sensomotorik, Ludwig-Maximilians-Universität München)

Abbreviations

2AFC	Two Alternative Forced Choice Task
AUC	Area under the curve
BOLD Response	Blood Oxygenation Level Dependent Response
CatCam	mobile eye-tracker for cat
DC/AC	Direct Current, Alternating Current
DES	Descriptive Experience Sampling
DKL	Derrington–Krauskopf–Lennie Colorspace
EEG	Electroencephalography
EI	Explicitation Interview
EyeSeeCam	Mobile gaze-contingent video eye-tracking system
fMRI	Functional Magnetic Resonance Imaging
FEW	Family Wise Comparison Error
FWHM	Full-Width-Half-Maximum
GOFAI	Good Old-fashioned Artificial Intelligence
GPS	Global Positioning System
HSV	Hue-Saturation-Value Colorspace
hMT+	Human Motion Complex +
HRF	Hemodynamic Response Function
JND	Point of Just Noticeable Difference
KL	Kullback-Leibler Divergenz
KSS	Karolinska Sleepiness Scale
MLE	Maximum-Likelihood Estimation
MoBi	Mobile Brain Imaging
MRI	Magnetic Resonance Imaging
MST	Medial Superior Temporal Cortex
MT	Medial Temporal Cortex
OKN	Optokinetic Nystagmus
PET	Positron Emission Topography
PPA	Parahippocampal Place Area
ROC	receiver operator characteristic
ROI	Region of Interest
rSTG	right Superior Temporal Gyrus
rTPJ	right Temporal Parietal Junction
S1 / S2	Primary / Secondary Somatosensory Cortex
SOD	Santa Barbara Sense Of Spatial Direction Scale
SPM	Statistic Parametric Mapping
STG	Superior Temporal Gyrus
REM	Rapid Eye Movement
T	Tesla
VBM	Voxel Based Morphometry
VIP	Ventral Intraparietal Cortex
VOR	Vestibular Ocular Reflex

List of Figures

Figure 1-1: Contribution to the feelSpace project.....	10
Figure 5-1: EyeSeeCam Setup.	88
Figure 5-2: EyeSeeCam Schematic View.	89
Figure 5-3: Example Movies.	90
Figure 5-4: Power Spectra	97
Figure 5-5: Topography of feature distributions.....	99
Figure 5-6: Gaze centres features.....	101
Figure 5-7: The EyeSeeCam recording setup and environments.....	113
Figure 5-8: Face-detection maps for the 9 different environments.....	115
Figure 5-9: Eye Positions in Laboratory Reply of Natural Movies.....	122
Figure 5-10: Spatial Distribution of Eye Position in Free Viewing and Laboratory Replay.....	125
Figure 5-11: Time Course of Eye Position in Static and Continuous Laboratory Reply.....	128
Figure 5-12: Average Saliency Maps Centered at Center of Gaze in Various Conditions.....	131
Figure 5-13: Discrimination from Saliency Model, Laboratory Model and Free Exploration.....	133
Figure 5-14: Video setup with gaze-driven and head-fixed scene cameras.....	146
Figure 5-15: Still frames of different environments.....	147
Figure 5-16: Gaze and Head velocity distributions.....	149
Figure 5-17: Relative movement of head and gaze; eye movement.....	151
Figure 5-18: Coordination of eye and head movements.....	153
Figure 5-19: Time-course of eye-head coordination.....	156
Figure 5-20: Time course of eye, head and gaze movements.....	159
Figure 5-21: Time constants of compensatory and synergistic movements.....	160
Figure 5-22: Accuracy and resolution of gaze camera positioning.....	166
Figure 5-23: Eye-position and velocity from servo control.....	168
Figure 5-24: Optimal compensation.....	169
Figure 5-25: Setup EyeSeeCam and CatCam.....	179
Figure 5-26: Velocity distributions.....	184
Figure 5-27: Eye movements and head movements.....	186
Figure 5-28: Temporal correlation.....	187
Figure 6-1: Piezo Actuator Housings.....	206
Figure 6-2: fMRI-Electronics and fMRI Belt.....	208
Figure 6-3: fMRI feelSpace Belt Setup for Electromagnetic Testing.....	209
Figure 6-4: Tests of Electromagnetic Artefacts or Heating of fMRI feelSpace Belt.....	210
Figure 6-5: Prototypes and Final Version of Mobile Piezo Actuator Belts.....	212
Figure 6-6: Indoor Homing Setup in Large Hall.....	221
Figure 6-7: VR Setp for Angular Self-Turning Experiment in the Cyberneum.....	225
Figure 6-8: Design of fMRI Homing Paradigm.....	234
Figure 6-9: Complete feelSpace fMRI Setup.....	235
Figure 6-10: Preliminary Analysis of feelSpace fMRI Pilot Data.....	239
Figure 6-11: Circular Interaction in Neurophenomenology.....	242
Figure 6-12: feelSpace Blind Pilot Study.....	255

List of Tables

Table 5.1-1: Environmente and Recoding Times	91
Table 5.4-1: Latency of Gaze Centred Camera in Dependence of Oscillation Frequency.....	165
Table 6.2-1: Candidate Neuronal Sides of Integration of Belt Information	231

Brief Contents

1	Acknowledgements	13
1.1	feelSpace.....	13
1.2	EyeSeeCam	14
2	Introduction	27
2.1	Motivation.....	27
2.2	Overview of The Present Thesis	28
3	Background	31
3.1	Cognitivism and Artificial Intelligence	31
3.2	Research Programs in Vision Research.....	37
3.3	Embodied Cognitive Science and Ecological Vision Research	49
3.4	Enactive Cognition and Perception.....	69
4	Summary and Discussion of Papers Represented in This Thesis	77
4.1	Salient Features at Gaze.....	77
4.2	Spatial Biases.....	77
4.3	Distinct Roles for Eyes- and Head in Allocating Gaze	78
4.4	Temporal Dynamics of Eye-Head Integration	79
4.5	Outlook.....	79
5	Appendix A: Publications	81
5.1	Study 1: Salient Features in Gaze-Aligned Recordings of Human Visual Input During Free Explorations of Natural Environments.	83
5.2	Study 2: Distinct Roles for Eye and Head Movements in Selecting Salient Image Parts During Natural Exploration.	109
5.3	Study 3: Gaze allocation in natural stimuli: comparing free exploration to head-fixed viewing conditions.	117
5.4	Study 4: Human Eye-Head Co-Ordination in Natural Exploration.	141
5.5	Study 5: Eye-Head Coordination During Free Exploration in Human and Cat.....	175
6	Appendix B: Other Projects	193
6.1	Visual Attention	195
6.2	Sensory Enhancement (feelSpace).....	199
7	Declaration	257
8	References	259

Contents

1	Acknowledgements	13
1.1	feelSpace	13
1.2	EyeSeeCam	14
2	Introduction	27
2.1	Motivation	27
2.2	Overview of The Present Thesis	28
3	Background	31
3.1	Cognitivism and Artificial Intelligence	31
3.1.1	The Core of the Cognitivist Research Program	31
3.1.2	Guiding Metaphors of Cognitivist Research	32
3.1.3	Practical Cognitivist Research	34
3.1.4	Critique	35
3.1.5	Two Classes of Embodiment Responses: Embodied Cognitive Science vs. Enactivism	35
3.2	Research Programs in Vision Research	37
3.2.1	Sensory Physiology of Vision	39
3.2.1.1	Holistic Feature Detectors and Ecological Vision	39
3.2.1.2	Local Feature Detectors and Computational Vision	40
3.2.2	Attention and Perception in Cognitive Psychology	43
3.2.2.1	Early Filter Models of Attention	43
3.2.2.2	Hierarchical Models of Attention and Perception	44
3.2.3	Visual Attention and Eye-Movement Control via Saliency Maps	45
3.2.3.1	Covert Visual Attention and Eye-Movement Control	45
3.2.3.2	Restrictions to the “Ecological Validity” of Saliency Research in the Laboratory	46
3.3	Embodied Cognitive Science and Ecological Vision Research	49
3.3.1	Ontogenetic Sensory Development	51
3.3.1.1	Sensory Development in the Light of Natural Stimuli	51
3.3.1.1.1	Statistical Properties of Natural Stimuli	51
3.3.1.1.2	Optimal Coding: Sensory Neurons as a Consequence of Natural Stimuli	52
3.3.1.2	Activity-Dependent Plasticity as a Physiological Basis of Sensory Development	52
3.3.1.2.1	Plasticity of Single Neurons	52
3.3.1.2.2	Plasticity of Neuronal Populations	53
3.3.1.2.3	Cross-Cortical and Multi-Modal Plasticity	53
3.3.1.3	Sensory Development in the Light of Actions	54
3.3.1.3.1	Sensory Plasticity as Sensorimotor Plasticity	54
3.3.1.3.2	Predictive Coding and Sensorimotor Contingencies	54
3.3.1.3.3	Intrinsic Motivation to Predict	55
3.3.1.3.4	Reafferents and Forward Models	56
3.3.1.3.5	Higher-Level and Motor Areas vs. Lower Level Areas in Perception	56

3.3.2	Visual-Spatial Attention of Acting Agents	57
3.3.2.1	Premotor Theory of (Visual) Attention	57
3.3.2.2	A Sensorimotor Account of Visual Saliency	58
3.3.2.3	Embodied Spatial Processing In a Three-Dimensional Action Space	59
3.3.3	Spontaneous Attention	61
3.3.4	Circuit Sharing in the Sensorimotor System: Embodiment of Higher-Level Concepts, Social Interaction and Language	61
3.3.4.1	Sensorimotor Metaphors in Language	62
3.3.4.2	Memory as Categorizing the Sensorimotor Space	62
3.3.4.3	The Perceptual Symbol Hypothesis	62
3.3.4.4	Circuit Sharing and Connectivity Analysis	63
3.3.5	Free Spontaneous Behaviour and Natural Data Recording - Methodologies for Ecological Neuroscience	64
3.3.6	Intermediate Summary	66
3.4	Enactive Cognition and Perception	69
3.4.1	Enactive Metaphysics: Neuro-Hermeneutics, Constructivism and Holistic Top- Down Causation	69
3.4.2	Autopoiesis, Autonomy, Adaption, Intrinsic Teleology, and Meaning Creation through Sense-Making	70
3.4.3	Mind-Life Continuity	71
3.4.4	Computational Implementations of Enactivism	71
3.4.5	Enactive Perception	72
3.4.6	Transmodal Inter-Subjective Perception	74
3.4.7	Enactive Attention And Saliency	74
4	Summary and Discussion of Papers Represented in This Thesis	77
4.1	Salient Features at Gaze	77
4.2	Spatial Biases	77
4.3	Distinct Roles for Eyes- and Head in Allocating Gaze	78
4.4	Temporal Dynamics of Eye-Head Integration	79
4.5	Outlook	79
5	Appendix A: Publications	81
5.1	Study 1: Salient Features in Gaze-Aligned Recordings of Human Visual Input During Free Explorations of Natural Environments.	83
5.2	Study 2: Distinct Roles for Eye and Head Movements in Selecting Salient Image Parts During Natural Exploration.	109
5.3	Study 3: Gaze allocation in natural stimuli: comparing free exploration to head-fixed viewing conditions.	117
5.4	Study 4: Human Eye-Head Co-Ordination in Natural Exploration.	141
5.5	Study 5: Eye-Head Coordination During Free Exploration in Human and Cat	175

6	Appendix B: Other Projects	193
6.1	Visual Attention	195
6.1.1	EyeSeeCam “Colour-Blind”	195
6.1.2	Empirical Saliency Matlab Toolbox	197
6.1.3	Empirical Saliency Baseline Study	197
6.2	Sensory Enhancement (feelSpace).....	199
6.2.1	Hypothesis	203
6.2.2	Belt Development	205
6.2.2.1	Magnetic Resonance Imaging (MRI) Compatible Piezo Belt.....	205
6.2.2.1.1	Tactile Actuators	205
6.2.2.1.2	Piezo-Housings.....	205
6.2.2.1.3	MRI-Compatible Cabling.....	206
6.2.2.1.4	MRI-Belt-Electronics & Electromagnetic Shielding	206
6.2.2.1.5	Optical-Control-Electronics	207
6.2.2.1.6	MRI-Compatibility Testing	207
6.2.2.1.7	MRI-Safety	207
6.2.2.2	Mobile Piezo Belt.....	210
6.2.2.2.1	Control-Electronics	210
6.2.2.2.2	Compass	211
6.2.2.2.3	Piezo-Driving-Electronics	211
6.2.2.2.4	Power Supply & Management	211
6.2.2.2.5	GPS.....	211
6.2.2.2.6	Mobile-Piezo-Housings.....	212
6.2.2.2.7	Electrical Insulation.....	212
6.2.2.2.8	Fire Protection	213
6.2.2.2.9	Water Protection.....	213
6.2.2.3	Mobile Pager Belt.....	213
6.2.2.4	Setup of Electronic Workshop and Internal / External Collaborations.....	213
6.2.3	Training.....	215
6.2.4	Physiological Integration: Sleep Electroencephalography (EEG).....	217
6.2.5	Behavioural Integration: Homing	219
6.2.5.1	Methods.....	220
6.2.5.2	Analysis.....	220
6.2.6	Optimal Multimodal Integration: Psychophysics	223
6.2.6.1	Methods.....	223
6.2.6.2	Analysis.....	224
6.2.7	Physiological Integration: Nystagmography	227
6.2.8	Cortical Integration: Functional Magnetic Resonance Imaging (fMRI).....	229
6.2.8.1	fMRI Hypothesis	229
6.2.8.2	Setup.....	232
6.2.8.3	Training.....	232
6.2.8.4	Procedure.....	233
6.2.8.5	Analysis.....	236
6.2.8.6	Regions of Interest (ROI).....	236
6.2.8.7	fMRI Acquisition	237
6.2.8.8	Voxel Based Morphometry	237

6.2.8.9	Conclusion.....	237
6.2.9	Qualitative Experience: Subjective Methods to Describe the View From Within	241
6.2.9.1	Neurophenomenology as Higher-Level Psychophysics.....	241
6.2.9.2	Explicitation Interview	243
6.2.9.3	Focusing / Thinking-On-The-Edge	244
6.2.9.4	Awareness-Trough-Movement.....	245
6.2.9.5	PRISMA	246
6.2.9.6	Descriptive Experience Sampling	247
6.2.9.7	Grounded Theory	247
6.2.9.8	Subjective Methodology for Sensory Enhancement	248
6.2.9.9	Sense of Direction Scale	249
6.2.9.10	My First-Person Experiences with the feelSpace belt.....	251
6.2.10	feelSpace Blind	253
7	Declaration	257
8	References	259

2 Introduction

*“To make discoveries, researchers need to look beyond the facts.”
(Shermer, 2012)*

2.1 Motivation

Six decades ago, the computational approach of cognitive science instigated a revolution in the studies of the mind. The prolific formative idea had been derived from logic and artificial intelligence and describes cognition in a computational way that can be implemented on computational machines. The so-called computational mind derives and manipulates symbolic representations of the environment, making inferences that aim to preserve logical truth statements about such representations to compute the best response of the organism to the current state of the world. As a major supposition, the mental realizes intelligent and meaningful behaviour through its independence from sensory and motor phenomena. The key to the mind is a universal computational machine that sits in between and gives meaning to sensation and action (Hurley, 1998). However, naturalizing the mind is a “hard problem” (e.g. Chalmers, 1995, 1996; Metzinger, 2000; Shear, 1999). It poses explanatory gaps between the mental and the physical that for conceptual reasons may resist explanation either in physical or in computational terms (Levine, 1983). For instance, the symbol-grounding problem, how abstract symbols can acquire their meaning, has been a major source of critique to the cognitivist program. Cognitive science has taken a positive attitude towards such foundational problems, and in response largely been driven by conceptual analysis and theory which then instigated novel empirical findings.

A prominent current theme is the theoretical re-evaluation of the role of sensorimotor processes for cognition, and the development of novel experimental paradigms for their investigation. Sensorimotor theories take inspiration from pragmatic philosophy, signal processing principles and neuronal plasticity to address problematic conceptual issues in logic and artificial intelligence. The pragmatic supposition is that cognition is not independent from but rather constituted in sensorimotor phenomena. Direct manipulation of sensorimotor processes situates the mental naturally in the world. Couplings between motor output and sensor input provide concrete, manifold and distinctively domain dependent relations of the organism to its environment. Sensorimotor contingencies are not defined in relation to logical truths about abstract symbols but in relation to the effects the organism’s actions have on its own perceptions while a situation unfolds. Physiological signal processing analysis highlights that the architecture of the brain adapts to such contingencies with remarkable plasticity at different time scales. Hence a sensorimotor view suggests that computations in the brain organize rather than interpret the couplings between system and world in an attempt to establish, maintain and enact couplings that are useful and adaptive in generating, preserving and achieving the goals of the organism within its world.

2.2 Overview of The Present Thesis

A promising phenomenon to study a sensorimotor nature of cognition is the way in which we couple our attention to the world through movements of our eyes and gaze. For a long time, eye-movements have been seen as an experimental link from behaviour to cognition and a “window to the mind”. Eye-movements relate cognition to behaviour by directing perception to selected aspect of a situation both in space and time. Yet surprisingly, despite the 20th anniversary of the “embodied turn”, sensorimotor approaches to visual attention are only in their beginnings. This thesis present a sensorimotor account of visual attention and eye movement control that conceptualizes visual attention not as a pre-selective low-level processing stage of object recognition, but as a global systems-level component within whole-body orientation that directs sensory and motor processes in the service of sensory and behavioural goals.

Pragmatic approaches highlight a need for novel experimental strategies that can investigate natural behaviour directly. When it occurs in the real world, natural behaviour instantiates interactions between physiological, embodied, situative and goal-directed aspects of sensorimotor processes. If a process such as attention is central to the organisation of these multi-layered interactions, then an exhaustive investigation requires sufficient ecological complexity in order to trigger naturally relevant interactions at the systems level in the experimental context. The main part of this thesis presents a novel pragmatic eye-tracking paradigm to study gaze and visual attention within the complexities of spontaneous natural behaviour. This novel paradigm yields video recordings of the visual perspective of human observers taken in real-world scenarios outside the laboratory. They closely approximate the retinal visual input of humans when eyes, head and body can freely interact in their natural ways with how a situation unfolds. Recordings thus capture the realistic human visual stimulation in its double role as a consequence of past and as an origin of future behaviour. These unique recordings of gaze allow to analyse spatial and temporal sensorimotor aspects of visual attention and gaze control under natural conditions.

The thesis is organized as follows. Chapter 4 summarizes the empirical research that forms the main part of this thesis. Chapter 5 presents the respective studies in detail. Prior to that, chapter 3 sketches a selective history of perception and cognition in cognitive science and neurophysiology that motivates the shift towards sensorimotor accounts of perception and attention. Chapter 3 is written to situate the empirical work of chapter 4 and 5 in a larger cognitive science context in accordance with the requirements of the PhD study regulations in Cognitive Science at the University of Osnabrück¹⁰.

Section 3.1 sets the general theoretical background. It starts with an introduction to the early cognitivist insight of internalist computational and representational mental processing. It then lays out the path of two general strands of pragmatic/embodied theoretical responses: (1) embodied cognitive science and computational neuroscience, both preserving the cognitivist core of computational analysis; and (2) enactivism, refuting the representational/computational analysis in favour of constructivist principles.

¹⁰ Promotionsordnung des Fachbereichs Humanwissenschaften für die Verleihung des Grade „Ph.D. in Cognitive Science“ vom 29.9.2011.

Section 3.2 outlines the cognivist eventually lead to models of perception that focus on constraints in computer vision at a cost of constraints from natural behaviour. This section argues that the seminal work of Hubel & Wiesel may be seen as a foundational bridge between physiological and computational aspects of vision. It started a transgression of visual physiology from early roots in signal processing and holistic constructivism to the immensely influential representational cognivist scheme. In particular, the dominant salience model of visual attention has been inspired by computer vision approaches as a lower level pre-stage for object recognition.

Section 3.3 explicates how pragmatic philosophy and models of neuronal plasticity based in signal processing theory form an alternative computational neuroscience of perception and action. Contingencies provided by the statistical structure in the world and in the organism's behaviour shape physiological signals. Processes of activity-dependent plasticity in turn form neuronal representations contingent upon the particular sensorimotor behaviour. Experiments on the role of top-down processing in perception, on sensory adaptation, on sensory substitution and sensory enhancement illustrate the role of behaviour at the perceptual level. While sensorimotor signal processing does adhere to the computational core of cognitive science, it understands representations as sensorimotor representations that discriminate aspects of the world subjectively in relation to behaviour rather than in relation to objective truth. This section argues that as a profound implication, visual attention and salient processes should be modelled as whole-body sensorimotor rather than purely sensory phenomena. Experimental implications that accompany this theory form the main motivation for the real-world approach to visual attention presented in the experimental part of the thesis (chapters 4 and 5).

Section 3.4 briefly explicates why the enactive approach to perception and cognition aims to pose a second strand of embodied and pragmatic theories that radically opposes computational analysis. Enactivism in part may be seen as a continuation of a second set of roots of sensory physiology in holistic-constructivism. The theoretical arguments of enactivism challenge the conceptual core of cognivism that links neuronal activity to representations and to the processing of information. As an alternative, enactivism introduces novel non-representational constructivist principles such as autopoiesis, autonomy and sense-making that are taken to "co-construct" rather than to "re-present" an organisms world. Current work in enactivism is beginning to expand these concepts for empirical research, and the end of this section briefly sketches a novel enactive conceptualization of attention and salience as aspects of sensorimotor sense-making rather than sensorimotor computation.

Section 4 summarizes and discusses the empirical publications. The reader only interested in the empirical work may directly begin with this summary on its own. Chapter 5 represents the publications in their original text.

Chapter 6 describes preliminary results of further projects, in particular of my work as project leader of feelSpace. Sensorimotor accounts of perception imply that perceptual modalities may not result from modality-specific cortical processing modules, but from plastic, modality-specific modes of sensorimotor organization using the discriminations provided by a sense organ. Sensory enhancement, as straightforward generalization, yields a stringent examination of this thesis. If true, introducing novel sensorimotor relations via an artificial sense organ should establish a novel perceptual modality. feelSpace supplies long-term directional information as vibro-tactile stimulation around the waist and investigates the resulting physiological and qualitative changes in perception in a set of behavioural, psychophysical, physiological as well as subjective measures. Since the main experiments are on going, they are presented as an appendix.

3 Background

This chapter situates the real-world eye-tracking experiment presented in chapter 4 and 5 in a larger cognitive science context to fulfil the PhD study regulations in Cognitive Science¹¹. Accordingly, it does not intend an in-depth historical review of cognitive science, which has been delivered elsewhere many times (e.g. Bechtel, 1988; Dupuy, 2009; Gardner, 1985; Stillings et al., 1995). Rather, this chapter provides a selective review, introducing cognitivism based on its analytical philosophical foundation and highlighting its historic empowerment by the mechanization of logic in the computational revolution and the failure of first-order cybernetics. It then motivates the more recent shift towards sensorimotor accounts via aspects of the mental that are emphasized in pragmatic philosophical approaches. It concludes with an argument for computational sensorimotor approaches that are accompanied by experimental strategies for real-world settings and an outlook to enactive approaches to cognition.

3.1 Cognitivism and Artificial Intelligence¹²

The cognitivist approach to the mind is founded in a long history of what philosophers of science call the analytical tradition of scientific inquiry (Hunt, 1999). The following aims to select a few relevant aspects of the analytic tradition that shaped the cognitivist understanding of cognition and perception which are in part both followed and questioned in recent theories of embodiment.

3.1.1 The Core of the Cognitivist Research Program

Analytic analysis is the epistemological attempt to understand a given domain of inquiry in atomic and context-free scientific theories. Analytic inquiry is a foundational explanatory program and seeks to describe a set of identifiable, well-defined basic properties and a set of general rules for their combination, such that a situation can be explained by the application of the rules on their constitutive parts. Part of the essence is that to fully explain a given domain, the explanation should not depend, neither as background nor constitutively, on any context outside of what is formulated in the theory (Morley & Hunt, 2000; Winograd & Flores, 1986). The analytic program had an upshot with the so-called computational revolution that also gave birth to the cognitive revolution in the study of the mind. With the Church-Turing thesis about a universal computational machine that can solve all computable problems¹³ (Turing, 1938) and von Neumann's implementation thereof, any computable function could in principle be mechanized¹⁴,

¹¹ Promotionsordnung des Fachbereichs Humanwissenschaften für die Verleihung des Grade „Ph.D. in Cognitive Science“ vom 29.9.2011.

¹² In this section I extend arguments presented in earlier work (Schumann, 2004).

¹³ While a precise treatment of computable problems is beyond this thesis, in a nutshell, the expression refers to all functions that are lambda-definable or Turing-equivalent.

¹⁴ However, this does not imply, that there may not be mechanical processes that are not Turing equivalent and thus necessitate a different approach to cognition. A contemporary debate for instance

giving causal power to logical form (Morley & Hunt, 2000). After a number of previous attempts in the philosophical history, when combining logic with computational machines, a genuine mechanization of mind for the first time seemed a real practical possibility and promising naturalistic contrast to Cartesian Dualism (Boden, 2006).

Perhaps the hardest challenge for an analytic naturalization of the mental is an account of intentionality (Brentano, 1874). Following philosophy of mind, what is distinctive of the mental over the physical is that mental states are inherently intentional. Mental states, unlike physical states, are about something and have genuinely meaningful content. Philosophers argue that seeing a car or feeling a pain is about the car or the pain in a way in which the involved physical processes are not, and this intentional aspect is an essential property of the mental that has proved difficult to naturalize. The cognitivist attempt walked down a particular route that can historically be seen as a response to the crisis of its predecessor, the program of first-order cybernetics (Boden, 2006; Froese, 2010, 2011). Ashby had shown that when the Wiener's cybernetic setting of mechanization via feedback loops and nonlinear dynamical systems is taken to its extreme, seemingly intelligent behaviour can be observed on the basis of random processes in the absence of the applicability of any reasonable agency concept or representation of meaningful internal states at all. Ashby's homeostat led the field into a crisis, the response to which co-founded cognitivism as a computational variant of the philosophical program of representationalism that equates meaningful mental processes with internal states, described in formal logic (Froese, 2010). That is to say, cognitivist research programs subscribe to the general representational argument that agents do not perceive the world directly but experience an inner representation thereof. The explanatory power of the cognitivist representationalist strategy as well as a main source of critique (section 3.1.5 and 3.4) is in the entailed abstraction from meaning via representations. The crucial representational step is that mental states are intentional, about things in the world, by virtue of representing objectively meaningful events in the world. The crucial computational step is that representations in turn can be described and mechanized by logical-symbolic descriptions that operate on a set of "context-free elements and some abstract relations among them" (Dreyfus & Dreyfus, 1988; cited in Hunt, 1999, p. 4). By combining representationalism and context-free analytic descriptions, taking care of syntax, which could now be done on machines, would also take care of semantics and intentionality (Morley & Hunt, 2000, Chapter 15, p.12). It led to the early conviction known as 'strong artificial intelligence' that "[within] a generation the problem of creating 'artificial intelligence' will be substantially solved" (Minsky, 1967).

3.1.2 Guiding Metaphors of Cognitivist Research

As Morley & Hunt (2000) argue, based on Imre Lakatos' work (Lakatos, 1976), core ideas of a research program, such as representationalism and computationalism above, are of metaphysical nature and not open for direct empirical testing, and hence the way in which they are further specified is a large part of what constitutes the nature and progress of a research program. From descriptive analysis, programs typically follow a set of further metaphors that guide the way the program progresses in response to experimental failure or theoretical developments.

suggests that Liquid State Machines (Maass, Natschläger, & Markram, 2002) may transcend Turing computation.

The metaphor most prominent in practical cognitivist research is that of the mind as a representational **information processing system** that “receives, stores, retrieves, transforms and transmits information” (Stillings et al., 1995, p. 1). A core debate that instigated enormous progress in cognitive science has been what counts as information and what a processing thereof. What is meant by information processing has been spelled out in a variety of ways, of which a few seem most influential.

The most disputable part common to these approaches is that they are variants of **representationalism** through the way they spell out intentionality by abstraction of meaning, to the extent that internal representational analysis has been considered the only game in town at the cost of neuronal and situational forces (Gardner, 1985). A less disputable part common to information processing systems is the use of internal structure, in some form or another, as “stands-in” for properties of the outside world (Bechtel, 1988), allowing the system a choice among a variety of alternatives by not cognizing and acting in the world directly (Winograd & Flores, 1986, p.97) as well as the use of environmental features when they are “not reliably present to the system” (Clark, 1997; Haugeland, 1991).

Newell and Simon’s **physical symbol hypothesis** emphasizes the computational value of a symbolic format of in the “specific architectural assertion” that “[syntactic] symbols lie at the root of intelligent action”. And that as a result, symbolic representational analysis is both necessary and sufficient for human-like intelligence as seen in problem solving (Newell & Simon, 1976, p.114). As a corollary, the concrete properties of the body are primarily a constraining factor on a system’s general symbolic computational abilities, and not an empowering source. The basis of the intuition is that processes within the concrete physical body are only an implementation of the causality-bearing level of computational processing that is required for action to be intelligent at the human level. In consequence, Newell and Simon also see neuroscientific research on the brain informative only in so far as it seeks to investigate the implementation of general symbolic computation in the brain, but explicitly not on its own rights, suggesting a high-level and top-down research strategy.

The division between the physiological and the computational has been directly explicated in neuroscience in Marr’s **tri-level hypothesis**, which takes up the point that the concrete functioning of the physical sensory hardware is relevant to a science of cognition in how it realises the algorithmic principles that implement the computations that the nervous system is envisioned to perform (Marr, 1976). A specific variant of this general computational approach to neuroscience had been proposed much earlier in McCulloch and Pitts’ seminal work in theoretical neuroscience described the function of **neurons as logical calculators** and the function of neuronal activity in a form of propositional logic calculations (McCulloch & Pitts, 1943). Already McCulloch and Pitts attempted to add a computational level to their physiological roots in signal processing (section also 3.2.1). Today, computational analysis is a target of much critique from embodied approaches to cognitive science, however, as the remainder will show, the contrast between physiological and computational analysis, however, is not as substantial as it is often described in the embodiment literature. What is problematic is not computational analysis per se, but its explicit linkage to general symbolic computational architectures. Computational analysis of embodied physiological processes, for instance in information theory, neuronal networks or probabilistic and Bayesian approaches (Knill & Pouget, 2004) shares the information processing core of the cognitivist program but provide alternatives to the symbolic-syntactic implementations. In fact, computational

neuroscience may be able to deliver contextual notions of symbols emerging from physiological signal processing signals, connecting both levels of analysis just as McCulloch & Pitts envisioned (König & Krüger, 2006).

Nevertheless, on the psychological side, symbolic analysis has been a major focus of cognitivism. Fodor's **computational theory of mind** assumes that thought must have a syntactic grammar to allow systematicity and productivity. Both properties, taken from formal language systems, were at the time considered fundamental to intelligent thinking in general (Fodor, 1975, 2000; Putnam, 1961). This goes well with Chomsky's **universal grammar**, a set of innate syntactic rules that the brain provides and which all languages share (Chomsky, 1965). In the notion of **general problem solving**, Newell and Simon further specify cognition as a type of rational thinking achieved by a set of general, domain-independent strategies that can be applied to any kind of domain. The main tools of cognitivist research hence are those of artificial intelligence and computational linguistics; algorithms for search, inference, problem solving or constraint satisfaction with accompanying logical formalisms for knowledge representation (Newell & Simon, 1961, 1972; S. Russel & Norvig, 2002). In particular problem-solving for a long time, was "generally taken for granted in artificial intelligence research" (Winograd & Flores, 1986, p.20ff).

3.1.3 Practical Cognitivist Research

In practical cognitivist research,

- general symbolic computation resulted in the practical search for an architecture of **context-invariant modules**, rather than an attempt to exploit concrete context-dependencies.
- cognition is approached as an **amodal process** operating on symbolic representations that are independent from the modal or cross-modal processes of perception and sensorimotor interaction.
- cognition engaged in **explicit computation**, since actions had to be instructed explicitly because behaviour was a result of cognizing exclusively on abstract internal maps and ontologies of the world.
- representations have to cover as many possibly relevant features of the world as possible, and most practical research problems chosen were instances of **offline-reasoning**, where it is possible to pre-plan the full action-sequence before action starts with the available technological resources.
- the early cognitivist program seemed more suitable for **static problems** such as chess or expert systems that avoid timely delicate interaction with the environment.
- studies of perception (in the orthodox literature not considered cognitive per se) and attention within cognitive psychology and neuroscience singled out selection mechanisms to **overcome informational bottlenecks** in deriving a representation of the world from the continuous overflow of information offered by afferent signals (see also section 3.2.2).

Overall, the resulting cognitivist picture of mind is that of a sequence of amodal symbolic mental states of a rather static, pre-planned nature that avoids time-critical interaction with the world. On the one hand, this is in contrast to a dynamical formulation of perception and action as

a set of skilled sensorimotor process that explicitly deal with the world in time (section 3.3) for which the present thesis provides an experimental paradigm in the real world (section 4). On the other hand, a static picture is not by necessity entailed in the computational core of the cognitivist program but may rather be a practical consequence of the formal tools of computation historically available as well as a consequence of the accompanying problems of higher-level abstract thinking to which there are particularly suitable.

3.1.4 Critique

The cognitivist program has seen an extremely influential rise, yet even main proponents speak of the failure of artificial intelligence (Fodor, 2000; in Rohde, 2008). Conceptual critique partly stems from the very conundrum cognitivism should resolve once first-order cybernetics had been considered a failure before: the intentionality of the mental. There is now a rising disbelief that syntactic representational analysis can do intentionality justice, so that despite all hopes, cognitivism in the end also would not address this central property of the mental just as first-order cybernetics (Froese, 2010). Given symbolic analysis, the **symbol grounding problem** formulates the question of how symbols and abstract representations could acquire their meaning within a concrete given context (Harnard, 1990). Providing solutions for symbol grounding is one of the central aspects of the embodiment literature. However, the **Chinese room argument** questions the central unification between meaning and intentionality and syntactic representations per se, arguing that the application of unintentional rules to unintentional symbols can only end up in equally unintentional results (Searle, 1980). Thereby it also renders any solution of the symbol grounding within a context-free representational program misguided.

Other problems stem from the concrete computational implementation. They form empirical-conceptual problems if conceptual problems addressed by computer science are taken as an empirical inquiry (Newell & Simon, 1976). The **frame problem** denotes the difficulty of tracking only relevant changes to the representational database after an action. Roughly speaking, updating a logical knowledgebase after action requires explicit update for all potential entries, even if most are untouched by the action. The **binding problem** is the difficulty of reconstructing objects in time and space based on free-floating features parsed in parallel from the world, the challenges of object segmentation, and differences in processing times of individual features (Treisman, 2003).

To give just two of the psychological empirical controversial points, it first is now argued that general problem solving is only a small fraction of what humans and biological organisms do in natural life. And further even humans are not particularly good at it but rather rely on **heuristic strategies** and ecologically **bounded rationality** also in the cases when they are faced with formal rational problems (Gigerenzer & Todd, 1999; Kahneman, 2003; Simon, 1972; Wason, 1966).

3.1.5 Two Classes of Embodiment Responses: Embodied Cognitive Science vs. Enactivism

Two broad classes of responses to cognitivism have been apparent. One is the idea of embodiment (section 3.3): to integrate the description of bodily and ecological context as well as their interaction into an analytic, computational theory of cognition. Including the context leads to

cognitive models that are embodied, distributed, situated or extended (Agre, 1997; Anderson, 2003; Brooks, 1991; Clark & Chalmers, 1998; Clark, 1997; Hutchins, 1995; Kirsh, 1996; Pfeifer & Bongard, 2006; Pfeifer & Scheier, 1999). Embodied extensions of the analytic program however may not be enough to ease Searle's above worries about intentionality if they remain meaningless elements of a now extended but nevertheless analytic and functionalist theory of cognition (Sharkey & Ziemke, 2001).

A more fundamental response is in the program of enactivism: the attempt to naturalize intentionality with a variant of second-order-cybernetic embodied theorizing (section 3.4). Enactivism is formulated in a non-representational manner that is closer to hermeneutical than the analytical tradition of inquiry (Froese, 2010; Kurthen, 1994; Stewart, Gapenne, & Di Paolo, 2011; Varela, Thompson, & Rosch, 1991) and to the systems biology of the organism (Froese & Ziemke, 2009). The enactive approach is influenced by work that has been termed dynamical (Beer, 2000; Port & van Gelder, 1994; Thelen & Smith, 1994), ecological (Gibson, 1979; Greeno, 1994; D. Lee & Kalmus, 1980), or situated (Clancey, 1997; Dewey, 1896). While clearly not all of these approaches share the enactive goal to naturalize intentionality, core enactivism in particular reflects a contemporary renaissance of the second-order cybernetic program with the wish to naturalize intentionality in a non-representational research program (Froese, 2010, 2011; Stewart et al., 2011; Thompson, 2007; Varela et al., 1991).

3.2 Research Programs in Vision Research

This section illustrates the influence of the cognitivist area on physiological research of vision. Initial experiments and models in sensory physiology were developed within the larger theoretical context of signal processing and holistic constructivism (section 3.2.1). But vision research has also made enormous use of cognitivist computational schemes of object recognition and information processing accounts of attention later on (section 3.2.2) and signal processing and computer vision approaches have developed in parallel over the years. This section argues that in particular the prominent salience model of visual attention (section 3.2.3) may be seen as a direct attempt to combine the physiology of feature detecting neurons with a computational solution to problems of cognitivist object formation.

The following section 3.3 aims to ground a sensorimotor account of visual attention in signal processing and embodiment rather than computer vision. Section 3.4 reflects on perception and attention within the constructivist program of enactivism. Both approaches suggest to complement laboratory experiments with experiments in real-world settings. The main experimental part of this thesis presents experiments within a novel approach to gaze-tracking in real-world settings, summarized in section 4.

3.2.1 Sensory Physiology of Vision

3.2.1.1 Holistic Feature Detectors and Ecological Vision¹⁵

Early experimental physiologists approached neuronal activity not as an implementation of logic, but as a signal-processing problem with its own right as an explanatory approach. They probed the activity in early sensory neurons for a correlation with the intensity of (spots of) light in order to understand sensory transduction principles (Barlow, 1953; Daniel & Whitteridge, 1961; Kuffler, 1953). Barlow launched the feature detector doctrine, but in contrast to truth-objective cognitivist representational thinking, he subscribed to an ecological mantra¹⁶ and considered feature detectors as holistic discriminators matched by evolution to the ecological structure of the world and relevant for individual behaviour (Martin, 1994).

A little later, another influential group approached neuronal activity directly within behavioural loops. Their famous experiments on fly detectors in the frog retina showed a role of spatio-temporal response characteristics of the frog retinal ganglia in the action-perception cycle of the frog catching a fly (Lettvin, Maturana, McCulloch, & Pitts, 1959).

Similar to enactivism and embodiment, both groups considered feature detectors holistic in that from the vast amount of ecologically available invariances, only those invariances that emerge in full behavioural loops are of discriminatory relevance and thus of interest to the nervous system. The function of the (sensory part of the) nervous system thus is to discriminate aspects of the world of the organism within its actions.

From the signal processing view the central physiological problem is how a nervous system can detect meaningful invariances in the presence of noise. Internal sensory and effector signals are not exact, and also situational affordances themselves contain a substantial amount of ambiguity that shows up as noise to the processing problem of the nervous system. For instance, even in the limited Umwelt of a frog only a subset of small moving things turn out to be flies that can be eaten. Barlow hence employed signal processing under noise and information theoretic analysis as computational approach to the functioning of the nervous system (Barlow, 1961; Martin, 1994).

The concept of information Barlow uses is not that of syntactic symbols in cognitivist artificial intelligence but Shannon's concept of information as a quantifier of the information transmitted in communication channels (Shannon, 1948). Barlow follows a representational explanatory strategy in subscribing information, in Shannon's sense, to an activity of the brain such as asserting spatio-temporal information to the frog ganglion cells. As Shannon information is related to signal transduction rather than to syntax, information theory and the naturally accompanying probabilistic approaches yield non-syntactic (minimally) representational approaches of embodiment.

¹⁵ Much of this section is taken from Kevin A. Martin's historical analysis of the feature detector (Martin, 1994).

¹⁶ Unfortunately, I could not find the reference for the term ecological mantra in this context anymore.

In contrast to Barlow, the group of Lettvin and Maturana espoused a constructivist, non-representational metaphysical interpretation of neuronal activity (Martin, 1994). In their view, the role of feature detectors is not and cannot be to represent information, knowledge or signals. Rather knowledge is constructed in the sensorimotor activities of the organisms and its environment in which feature detectors and nervous system participate y allowing more complex discriminations. Taken up in particular by Maturana and Varela (Maturana & Varela, 1992) this program today is continued under the headline of enactivism that might also be seen as a successor of second-order cybernetics (Froese, 2010).

3.2.1.2 Local Feature Detectors and Computational Vision

With Hubel & Wiesel's seminal discovery that oriented bars or edges were much better stimuli than patches of light for sensory cells in the cortex (Hubel & Wiesel, 1959), the relation between the detailed structure of stimuli features to neuronal features (rather than to behaviour) moved into the centre of physiological interest. Departing from holistic features and behavioural loops, Hubel and Wiesel switched the focus to local aspects of stimuli such as bars, edges, colour, depth, and so on. Their research strategy presented parametric variations of simple artificial stimuli and derived many important properties of sensory neurons, such as the precise mappings of many receptive field properties (Livingstone & Hubel, 1988). Receptive field mapping still has a large influence on the field. Hubel & Wiesel's choice of simplified stimuli (e.g. only one spatial frequency at a time) and the apparent lack of behaviour (animals were fixed to allow precise recordings) had reasons in the technical limitations of the period. Artificial stimuli are comparatively simple to generate and mathematically well described. However, leading commentators (Martin, 1994) see a main reason for the use of artificial stimuli also in a compositional conceptualization of perceptual neuronal activity that eventually emerged. Hubel and Wiesel assumed that the nervous system decomposes the natural world into atomistic components and a set of rules of grouping (Livingstone & Hubel, 1988). It is not fully clear from Martin's work whether or not Hubel & Wiesel themselves made reference to artificial intelligence and Martin strongly suggests that they had an exceptional level of cautious reluctance to interpret their own work beyond the experimental evidence given. Yet, a compositional strategy in physiology of course did go well with the compositional cognitivist explanatory strategy being made prominent by artificial intelligence not much after. Indeed, compositional vision had been worked out on theoretic grounds as a means to derive arbitrary complexity from the limited resources of physiological hardware (Minsky, 1961; Neisser, 1967; Pitts & McCulloch, 1947, see section 3.2.2). In the seventies linear systems theory described cells in primary visual cortex as linear convolution filters for the spatial frequencies of stimulus patches (Campbell & Maffei, 1974; Shapley & Lennie, 1985), and this lay a ground to combine feature detectors and computational vision explicitly. Marr and Poggio's symbolic compositional-representational theory of vision suggested elements of logic and artificial intelligence for mainstream visual neuroscience (Marr, 1976). Similar to Newell and Simon's physical symbol hypothesis, Marr established a symbolic computational level of analysis as the level of abstraction that explains what neuronal physiology is doing (Marr, 1976). Today the influence of Marr's work on the computational analysis of experimental research continues to foster the fields of computational and cognitive neuroscience (Willems, 2011) albeit making use of different forms of (non-syntactic) computation and with more appreciation for the importance of physiological detail for the

computation being performed (Abbott, 2008). Equally, the cognitivist predicament of decomposing everyday perception into neuronal responses to simple artificial stimuli continues to inform large parts of mainstream neuroscience of vision in important ways (Riesenhuber & Poggio, 1999).

3.2.2 Attention and Perception in Cognitive Psychology

This section highlights how information processing considerations influenced models of perception of attention. The concept of attention, in vision and otherwise, has a long history within psychology, mostly formulated as a way of managing mental resources that are limited. In the introspective words of William James, attention is the

“taking possession by the mind, in clear and vivid form, of one out of what seem several simultaneously possible objects or trains of thought. Focalization [and] concentration of consciousness are of its essence. It implies withdrawal from some things in order to deal effectively with others, and is a condition which has a real opposite in the confused, dazed, scatterbrain state” (James, 1890, p. 403-404).

Psychoanalysis developed the idea of resource management into a model of attention as a way of channelling limited amounts of psychic energy (Neisser, 1967). Similarly, cognitivist research interpreted the metaphor of limited resources, within its own metaphysical background, as a way of dealing with limited computational resources in the processing of information (for an early but still influential review see Neisser, 1967).

3.2.2.1 Early Filter Models of Attention

Information processing models of attention begin from an obvious starting point: it is certainly true that sensory systems, in information theoretic terms, provide an excess of signals. The eyes alone may deliver about 10 million bit/s to the nervous system (Norretranders, 2002). The filter model was the first conceptual proposal of how attention processes help the brain to deal with this overabundance of information. The rationale was that if the resources of semantic processing are limited to a fixed capacity, attention needs to filter out irrelevant signals in early sensory channels based on pre-cognitive sensory features such as source location, bandwidth or intensity (Broadbent, 1958). Initial experiments in dichotic listening supported the suppression of unattended signals (Cherry, 1953), but later experiments revealed semantic analysis of unattended messages (Treisman, 1964) rendering the envisioned model of an early filter too simple. On the one hand, to the degree to which a signal filter is based on complex measures of relevance/irrelevance, it is likely to require the semantic processes of normal perception in the first place, pushing the filter to late stages of the processing chain (Deutsch & Deutsch, 1963). On the other hand, late filtering loses its economic effect of cleaning out massive amounts of sensory data before cognitive processing, such that it seemed more plausible to assume that a filter would only attenuate rather than block sensory signals to lower their signal-to-noise ratio (Treisman, 1964). Semantic analysis then could employ a signal-detection process to define a perceptual threshold along dimensions relevant to the current state of semantic processing and reject signals below the threshold as noise. Yet if the threshold for filtering would be lowered along another dimension, for instance by contextual information, signals would no longer be rejected as noise but passed on to further processing.

3.2.2.2 Hierarchical Models of Attention and Perception

The debate about attention as a filter was eventually transformed by the formulation of hierarchical models of perception. Hierarchical models aimed to resolve a mirror debate between analytic (~ bottom up) and synthetic (~ top-down) approaches to perception. Gestalt psychologist argued that the perceptual whole precedes its parts, but found it difficult to explain how Gestalts are established. Prominent analytical perceptual models in physiology (Hebb, 1949; Klein, 2011) or machine learning (Selfridge, 1958) showed prospects for the recognition of individual objects but failed in the sensory presence of multiple objects as simple as two triangles. The hierarchical combination of both approaches sequentially restricts object segmentation to one location of the image at a time such that a later synthetic integration stage can bind current sensory features of objects making in sequence, also making use of prior hypothesis about typical forms of objects (Minsky, 1961).

In this hierarchical approach, attention is not a filter, but a sequential mechanism that directs the limited capacities of synthetic binding processes to a few objects at a time (Neisser, 1967). Local stimulus features reach the level of perception when bound into the current percept, but can remain “free floating” in the system otherwise without being actively filtered out or suppressed. Evidence for sequential physiological activation dates again to Hebb in his formulation of “phase sequences”, the suggestion that sequential activation of neuronal cell assemblies forms the neuronal correlates of conscious thought (Hebb, 1949; Klein, 2011). Psychophysical evidence for sequential processes in vision comes from the highly influential Feature Integration Theory (Treisman & Gelade, 1980). Experiments show that a location only captures attention automatically, such that it “pops-out” in awareness, if the location is distinctive by bottom-up analysis of its low-level features alone. However, if the feature set is homogeneous over the entire visual field, sequential direction of focal attention over the stimulus is required to perceive objects in sequence. This confirmed a sequential synthetic integration of features into coherent wholes for each location in turn on the psychological level, after it had been introduced for computational reasons in Minsky’s model of object recognition (Minsky, 1961).

Research on attention has now formed a huge field of its own, in particular with respect to its neuronal underpinnings (Treue, 2001). A broad majority of the neuroscientific research paradigms on attention are essentially founded in the legacy of the information-processing conceptualization of attention. They for instance draw their operationalization of attention from behavioural increases or decreases of task performance that are related to processing capacities of serials bottlenecks and they often perform experiments in artificial paradigms shaping the questions asked in experiments and the answers found in information-processing ways (Cosmelli, 2009).

3.2.3 Visual Attention and Eye-Movement Control via Saliency Maps

With respect to visual attention, a central contemporary topic concerns how attention sequentially selects one region over another. The most prominent control model is the saliency model of Ullman and Koch (Koch & Ullman, 1985). Merging the physiology of Hubel & Wiesel's feature detectors with the computational arguments for hierarchical object recognition, the saliency model computes low-level features as sequential filters in parallel channels and at various spatial scales. Contrary to Treisman's psychological model, however, in the absence of attention features do not end up as free-floating representations but are always spatially bound into a global map within pre-attentive parts of the visual processing chain. Given the centre-surround receptive field principles of neuronal feature detectors, these maps represent how much a region differs from its neighbouring regions in an information theoretic measure of interestingness of the respective part of the (visual) world. Saliency maps represent the parts of the visual stimulus where pre-attentive bottom-up analysis predicts most information. Focal attention shifts in a winner-takes-all mechanism to the most interesting location as predicted exclusively by such bottom-up saliency. The selected location then enters synthetic object processing and perception. Subsequent inhibition-of-return principles deactivate the current position, and focal attention directs processing to the second most salient region, and so forth. Hence, the saliency model is a bottom-up generative model for sequences of visual attention shifts, which in every shift select the region that according to the saliency representation of the world should yield most information. The claim is that bottom up saliency is a physiological mechanisms that determines what regions of space capture visual attention.

3.2.3.1 Covert Visual Attention and Eye-Movement Control

There is a strikingly obvious parallel between computational arguments for sequential focal attention in visual processing and the biology of sense organs, which, surprisingly, has been explicated only relatively recently. Computational arguments instigated hierarchical models of perception with sequential local processing of individual regions such as the saliency model. Likewise, many mammalian species in fact have a region of highest retinal acuity that covers a small focal part of their visual field (e.g. in cats about 5° and in humans about 1° visual angle) and dominates the input into in the adult visual system (Rapaport & Stone, 1984). This requires a movement of gaze to pick up detailed information from the environment already at the level of the sense organ, which mirrors shifts in covert focal attention at the level of perceptual processing. Hence, recently the attention concept of saliency has been suggested as a computational generative model for eye movements as well (Itti & Koch, 2001; Moore, Armstrong, & Fallah, 2003; Treue, 2003). In turn, observed overt attention (shifts of the sense organ) have been taken as an operational proxy for covert attention (shifts in internal focus) in experiments on visual attention. This argument takes computational constraints to interpret the functional role of the fovea. However, the interpretation from a certain (cognitivist) computational theory in a restricted domain (of object representation) might over-emphasize the actual dominance of both the fovea and visual object perception for behaviour. From a pragmatic theoretical perspective that sees the major role of the brain not in object perception but in organizing whole-body behaviour, for instance peripheral retinal signals for movement or the coarse orientation of gaze via movements

of body and head are likely to play a major role in visual behaviour of the organism as well. Part of a pragmatic view is that computational modelling should be guided by the phenomenon as it naturally occurs in order to obtain realistic models, for instance in studying visual attention in behaviour at the systems level.

In fact, the salience model has been confirmed as a model of eye-movement control in a vast number of empirical studies that find that gaze locations on natural images correlate with the presence of low-level features such as luminance contrast (Reinagel & Zador, 1999), edge density (Mannan, Ruddock, & Wooding, 1996, 1997; Tatler, Baddeley, & Vincent, 2006) and texture contrast (Einhäuser & König, 2003; Parkhurst & Niebur, 2004). Saliency maps to some extent even can predict gaze allocation on images exclusively on the basis of stimulus features (Parkhurst, Law, & Niebur, 2002; Peters, Iyer, Itti, & Koch, 2005; Wilming, Betz, Kietzmann, & Ko, 2011). But nevertheless, salience researchers currently recognize that bottom-up signal processing is only one source in a complex mechanism of visual-spatial attention that also includes top-down factors such as task, history, semantics and prior experiences of the organism. Hence in recent years a decisive role in eye-movement control has been given to higher-order correlations within images (Krieger, Rentschler, Hauske, Schill, & Zetsche, 2000), contextual cues (Torralba, Oliva, Castelhana, & Henderson, 2006), and objects such as faces (Cerf, Harel, Einhäuser, & Koch, 2008). Similarly, early studies demonstrated the importance of tasks for eye movements on images (Buswell, 1935; Yarbus, 1967) and recent experiments show that modern bottom-up models may lose all their predictive power (Henderson, Brockmole, Castelhana, & Mack, 2006; Rothkopf, Ballard, & Hayhoe, 2007) and bottom-up cues may be immediately overruled or even reversed (Einhäuser, Rutishauser, & Koch, 2008). In consequence, very recent work on saliency mapping of images concerns the combination of bottom-up saliency with top-down biases considering the task of the system (Hamker, 2006; Navalpakkam & Itti, 2007; Pomplun, 2006; Rutishauser & Koch, 2007).

3.2.3.2 Restrictions to the “Ecological Validity” of Saliency Research in the Laboratory

Also, the “ecological validity”, or representative design¹⁷ of saliency research - the degree to which it reflects processes of visual attention and gaze control in natural settings - is under serious debate. Tests of saliency models are typically performed in head-restrained laboratories, which are restricted to eye-in-head movements, do not allow real-world interactions, involve a potentially biased choice of stimuli (e.g. photographers bias), which are mostly static, presented in a restricted field of view, and contain a highly unnatural frequency of scene onsets due to the sequential presentation of static images (Torralba et al., 2006).

Similar restrictions are part of saliency models themselves. Saliency models assume visual input to be a sequence of quasi-stable saccades, and in consequence yield a quasi-static rendition of attention. Saliency maps provide a representationalist mapping of the world in terms of atomistic visual features derived in a bottom up manner on top of which a minimal cognitive

¹⁷ The term “ecological validity“ was originally applied by Brunswick as a statistical measure for the correlation between a proximal stimulus cue (which the nervous system can detect by it’s senses) and an aspect of the distal stimulus (the origin of the cue in the world). It is now often used to describe what Brunswick termed representative design - the degree to which an experiment transfers to real-life settings (Brunswick, 1955; Dhimi, Hertwig, & Hoffrage, 2004). I am thankful to Frank Jäkel for this reference.

process, a winner-takes-all decision rule, instructs the behavioural output of the eyes. This in essence is the cognitivist input-output sandwich in operation, which puts cognition in between perceptual representations and instructions for action (Hurley, 1998). The winner-takes-all-ruling on the spatial saliency map is neutral with respect to intentional action, does not address how the direction of gaze coordinates body and head with eyes while each is interacting non-visually with the world on their own generating interactive motor constraints on gaze allocation. The principle of inhibition-of-return is only computationally but not empirically motivated as people do frequently return to or stay at visited locations without entering circular loops (Tatler, Hayhoe, Land, & Ballard, 2011). Saliency theory is uni-modal in its theoretical formulation as well as in laboratory experiments despite the multimodal nature of spatial processing and prefrontal action control (see 3.3.2) where in particular vestibular information is of crucial importance (Andersen, Snyder, Bradley, & Xing, 1997; Angelaki & Cullen, 2008; Ghazanfar & Schroeder, 2006). In addition, goal-directed ecological behaviour in natural environments suggests more fluid and embodied concepts of attention and perception that challenge a simple representational picture of vision per se (see section 3.3). Ecological vision involves dynamical spatial processing and continuous task-driven coordinate transformations that go beyond the passive image-based representational assumptions of saliency mapping (section 3.3.2). Lastly, eye movements are a core part of almost all of everyday actions also on higher-level cognitive and social levels (Land & Hayhoe, 2001). Thus they have been characterized as a “window to the mind”¹⁸ rather than as window to (bottom-up) salience of the world. Hence in natural behaviour movements of gaze are likely directed by sensory features that are actively picked up in the light of procedural task knowledge that is currently being played out (see section 3.3.1.3, 3.3.2, 3.3.4). These pragmatic considerations demand salience-based models of gaze allocation to modified for and tested within in less restrained settings within natural environments. All of these pragmatic aspects will be explicated in more detail in the next section.

¹⁸ Unfortunately I could not find the definite source of this common expression.

3.3 Embodied Cognitive Science and Ecological Vision Research

The following section introduces a predominant response to the various critiques of the syntactic-cognitivist research program: the inclusion of body and world into an analytic and computational theory of cognition. One of the roots of pragmatic thinking is a famous paper by 19th century pragmatic psychologist John Dewey, arguing that

“[perception] begin[s] not with a sensory stimulus, but with a sensorimotor coordination ... and that in a certain sense it is the movement which is primary and the sensation which is secondary, the movement of the body, head and eye muscles determining the quality of what is experienced. In other words, the real beginning is with the act of seeing; it is looking, and not a sensation of light” (Dewey, 1896, p. p358-359)

Another root is in phenomenology, such as the work of Merleau-Ponty, who derives that

“since all the stimulations which the organism receives have in turn been possible only by its preceding movements which have culminated in exposing the receptor organ to external influences, one could also say that behaviour is the first cause of all stimulations. Thus the form of the excitant is created by the organism itself” (Merleau-Ponty, 1962, p. 211).

The following presents attempts to re-connect the program of the mechanization of thought by information processing to a long history of pragmatic and ecological traditions, with a concept of information derived from signal processing and theories of optimal coding. In its conclusion, this section outlines a pragmatic sensorimotor-account of visual attention and gaze-control.

3.3.1 Ontogenetic Sensory Development¹⁹

Barlow's ecological take on physiology in section 3.2.1 proposed that the brain develops as an optimization of the signals neurons are exposed to at evolutionary, developmental and behavioural timescales. Describing optimization in information theoretic terms lead to the field of optimal coding which, as Simoncelli & Olshausen point out (Simoncelli & Olshausen, 2001), considers sensory development as an ontogenetic learning process that aims to optimize neuronal responses to a set of three fundamental constraints: (1) the statistical properties of the natural environment of an organism, (2) the physiological properties of the neural hardware, and (3) the tasks and the statistical (sensory-) consequences of the organism's behaviour. All three aspects in particular may be developed into an information processing account of the pragmatic program of Dewey and Merleau-Ponty. Each aspect will be considered in turn.

3.3.1.1 Sensory Development in the Light of Natural Stimuli

3.3.1.1.1 Statistical Properties of Natural Stimuli

Barlow's signal processing approach to sensory physiology is based on the fact that the natural (visual) world is not a random combination of pixels but consists of complex structures and redundancies in first- and in particular in higher-order statistics to which the brain is likely to adapt its processing (Barlow, 1961). For instance, the power spectrum of natural images is not uniform but typically falls with a $1/f^2$ relation for higher frequencies. Barlow was among the first to suggest that in an information theoretic sense, the brain uses its signal processing resources in a statistically optimal way when it reduces this redundancy such that each neuron carries the same amount of information about its domain, a view known as sparse coding. Subsequent research could empirically demonstrate this coding principle, for instance with the finding that the LGN de-correlates the $1/f^2$ relation, with the consequence that neuronal responses are modulated to better differentiate between those frequencies more commonly found in natural images (e.g. Dan, Atick, & Reid, 1996). Similar de-correlation and sparse coding has been found in other parts of the visual hierarchy as well, such as for example for the orientation of bars in V1 (e.g. Vinje & Gallant, 2000).

Barlow envisioned that the spatial statistical structure of the natural environment would lead to massive contextual modulations of neuronal processing (Barlow, 1961). Work of the last decade indicates that single neuron behaviour is not defined in isolation by properties of the world but subject to modulation by contextual occurrence of other stimuli outside classical receptive fields, and also by global top-down factors and on-going internal activity in non-linear manners (e.g. Salinas & Sejnowski, 2001; Trotter & Celebrini, 1999; Vinje & Gallant, 2000). This means that in direct violation of Hubel & Wiesel's compositionality assumption (section 3.2.1.2), neuronal responses to natural stimuli are not well predicted by what has been learned about

¹⁹ A substantial part of this section is taken from my final draft of the grant proposal for the feelSpace project „Sensory enhancement — learning a new sense“ to Deutsche Forschungsgemeinschaft (DFG).

responses to simple stimuli (for a review see Moldonado, Ossandon, & Flores, 2009; Yen, Baker, & Gray, 2007).

3.3.1.1.2 Optimal Coding: Sensory Neurons as a Consequence of Natural Stimuli

Since the time of Barlow, much progress has been made on the theoretical side of neuronal signal processing using technical possibilities only recently available. Important neuronal properties could be theoretically derived as a statistical consequence of the structure of natural images. Learning the spatial correlations of natural images in an unsupervised manner can reveal non-trivial receptive field properties of simple cells (Bell & Sejnowski, 1997; Lewicki & Olshausen, 1999; Olshausen & Field, 1996, 1997; van Hateren & van der Schaaf, 1998) and complex cells (Hyvärinen & Hoyer, 2001; Körding, Kayser, Einhäuser, & König, 2004). Unsupervised learning of other (e.g. temporal) statistical properties in natural visual input could give rise to many of the response properties in distinct layers of hierarchical models as one moves upward in the ventral visual system (Kayser, Körding, & König, 2004). A very recent discovery is the unsupervised formation of location sensitive cells akin to hippocampal place cell or head-direction cells from the statistics of natural visual input of a behaving agent (Franzius, Sprekeler, & Wiskott, 2007; Wyss, König, & Verschure, 2006). Also sensory development in non-visual modalities has been modelled by unsupervised learning of the respective input statistics. Learning the properties of natural sounds leads to non-trivial predictions of auditory neurons' receptive fields (E. C. Smith & Lewicki, 2006). In the whisker system, some properties of neurons in the barrel cortex can be predicted by learning the properties of whisker signals, and used for texture discrimination (Hafner, Fend, König, & Körding, 2004; Hipp, Einhäuser, Conrads, & König, 2005).

3.3.1.2 Activity-Dependent Plasticity as a Physiological Basis of Sensory Development

Complementary to the advances of models of unsupervised coding of the statistics of natural stimuli, substantial progress has also been made regarding the underlying physiological mechanisms. Pivotal work was the postulate by D.O. Hebb (1949) that effective connectivity changes according to the success of one neuron in activating another neuron; or in colloquial terms "what fires together wires together". Spurred by the discovery of activity dependent plasticity (Bliss & Lomo, 1970) and the characterization of the role of back-propagating action potentials in this process (Markram, 1997) interest in this area exploded (Pascual-Leone, Amedi, Fregni, & Merabet, 2005). The following selects relevant aspects of plasticity for a sensorimotor account of perception and attention.

3.3.1.2.1 Plasticity of Single Neurons

At the cellular level, an important aspect of plasticity and sensorimotor learning is the relative separation of different signal integration sites. The coincidence of a back-propagating action potential with input to the apical dendritic tree leads to a sequence of events separating inputs from different sources (Larkum, Zhu, & Sakmann, 1999; Siegel, Körding, & König, 2000; Stuart & Sakmann, 1994). Furthermore, local synaptic mechanisms are subject to global influences from nonspecific modulatory systems (Kilgard & Merzenich, 1998). These phenomena are

naturally described by learning rules based on individual neurons with two sites of integration that lead to an interaction of local and global processes (Sanchez-Montanes, Verschure, & König, 2000).

3.3.1.2.2 Plasticity of Neuronal Populations

On the population level, cortical (re-)organization in response to input activity has been shown in all sensory domains. Cortical representations change due to passive sensory experience, deprivation of input by peripheral lesions, and training on sensory tasks (Buonomano & Merzenich, 1998; Feldman & Brecht, 2005; Kaas, 1991). To give a few prominent examples, in the somatosensory system the representational sites of rat whiskers and finger digits in monkeys and professional musicians grow with experience (Elbert, Junghöfer, Scholz, & Schneider, 1995; Jenkins, Merzenich, Ochs, Allard, & Guic-Robles, 1990). Similarly, extensive training of pitch discrimination in the auditory system increases the volume of the Heschl gyrus (P. Schneider et al., 2002, 2005). In the visual system, lesioning retinal input changes the retinotopic organization from the LGN upwards to primary and extrastriate visual cortex, with neurons taking over retinal areas adjacent to the lesion (Eysel, 1982; Heinen & Skavenski, 1991; Kaas, 1991; Krubitzer & Kaas, 1989). Plastic processes also underlie the development of the olfactory and the gustatory system (Hill, 2004; Wilson & Mainen, 2006). Hence, plastic processes that dynamically organize neural topography have been demonstrated in all sensory systems, and may form a general principle of neural functioning.

3.3.1.2.3 Cross-Cortical and Multi-Modal Plasticity

Further, sensorimotor relations are inherently multi-modal, and also interactions between cross-cortical multimodal areas are formed by signal-driven plasticity. Studies rerouting visual connections into auditory structures at early processing levels suggest that orientation- and direction-specific ‘visual’ cells arranged in an orderly retinotopic map can develop even in the auditory cortex (Sur, Garraghty, & Roe, 1988). Remarkably, these rewired ferrets respond to the visual stimuli as if they perceive the stimuli to be visual rather than auditory (Von Melchner, Pallas, & Sur, 2000). Similarly not only the auditory but also the visual cortex can learn new functionality given different input (Gilbert & Walsh, 2004). In congenitally blind humans, the primary visual cortex processes somatosensory information (Büchel, Price, Frackowiak, & Friston, 1998; Büchel, 1998; Cohen et al., 1997; Kupers et al., 2006), while extrastriate visual areas are involved in the processing of auditory information about space (Collignon, Lassonde, Lepore, Bastien, & Veraart, 2007). Moreover, involvement of the visual cortex in language and memory can be demonstrated in the congenitally blind (Amedi, Floel, Knecht, Zohary, & Cohen, 2004; Amedi, Raz, Pianka, Malach, & Zohary, 2003). Even in sighted individuals the visual cortex can engage in tactile processing, given extensive training (Merabet et al., 2007; Saito, Okada, Honda, Yonekura, & Sadato, 2006). These studies reveal a remarkable plasticity and thereby flexibility in the involvement of cortical areas in the processing of different modalities.

The picture that emerges is that development of cortical areas to a large extent relies on ontogenetic learning of the respective activity-patterns of (cross-modal) signal statistics, drawing upon the anatomy provided phylogenetically (Horng & Sur, 2006; Sur & Leamey, 2001). Consequently, the functionality and connectivity within the brain is not primarily defined by anatomy or sensory apparatus but by the properties of the information being processed.

As a corollary, what sensory features of the world an animal is likely to be well-adapted to detecting is an empirical-statistical matter as well. In part defined by the structure of the organism's natural world, and in part by the learning possibilities provided by brain physiology.

3.3.1.3 Sensory Development in the Light of Actions

3.3.1.3.1 Sensory Plasticity as Sensorimotor Plasticity

The following will show the influence of behaviour on the structural and functional plasticity of the sensory system. Active, self-initiated behaviour is a major source of the signal statistics neurons adapt to. But the mere exposition to signals in the (multimodal) sensory space seems not enough for many aspects of neuronal development, and hence active behaviour seems a more foundational requirement for essential aspects of sensory plasticity. The much-cited experiments of Held indicate that passively moved kittens that are prevented from active self-exploration do not develop normal sensory processing abilities, even if they received identical sensory stimulation than a self-exploring kitten (Held, 1965). The implication is that the major part of sensory plasticity and development is in fact not only of a sensory nature but instead a process of sensorimotor plasticity that is only triggered given sufficient self-guided experience. A similar finding comes in Kohler's equally well-known experiments on inverting prism adaption (Kohler, 1962) where the initial distortion of perception induced by a prism can, remarkably, slowly revert back to normal in some (but not in all) aspects of perception. Also prism adaption requires sufficient active exploration of the altered sensorimotor relations. The paradigm of sensory substitution showed that it is possible to deliver signals of one modality (e.g. vision) to the brain via a second interface modality (e.g. tactile), and that the perception of the signal can re-establish perceptual qualities of the source modality, but again only with sufficient active exercise of the novel sensorimotor relations (Bach-y-Rita, 1972, 2004). Active also seems essential for sensory enhancement (see section 6.2), where a novel signal such as the direction of magnetic north (Nagel, Carl, Kringe, Martin, & König, 2005) or a measure of spatial distance (Cassinelli, Reynolds, & Ishikawa, 2006; Froese, McGann, Bigge, Spiers, & Seth, 2011; Siegle & Warren, 2010) is supplied over an interface modality and can yield a novel perceptual quality, but only with active exploration of the relations between the novel sensory signal and action.

3.3.1.3.2 Predictive Coding and Sensorimotor Contingencies

Much like the structure in the natural world, the relations between sensory signals and actions are not random, but inherit common transformation structures that have recently been termed "sensorimotor contingencies". Gibson's work on optic flow describes how perception actively uses these dependencies between behaviour and sensation as ecological control variables (Gibson, 1979). In an recent influential paper, O'Regan and Noë extended this hypothesis and suggest that skilled mastery of knowledge about changes in sensory activity is a general principle that constitutes the perception of objects (O'Regan & Noë, 2001). O'Regan & Noë posit the concept of skilled mastery of sensorimotor relations in contrast to representational sensory processing, in particular to the syntactic symbols of artificial intelligence.

However their central notion of knowledge about sensorimotor contingencies does in fact suggest a representation of (sensorimotor) knowledge within the sensorimotor system (Clark, 2006) and has been fruitfully approached in computational neuroscience. Learning sensorimotor contingencies can for instance connect grasping movements associated with objects to their visual representation to help perception infer the shape of an object (Hoffmann et al., 2005; Hoffmann, 2007). Organisms can extract fundamental properties of space without prior knowledge from regularities in their sensorimotor space (Philipona et al., 2003, 2004). Unsupervised learning with objective functions for optimal coding can directly be extended to learn predictions about activity changes in lower (König & Krüger, 2006) or higher sensory areas (Weiller, Martin, Dähne, Engel, & König, 2010). For instance, the higher-level concept of place fields can not only be derived “bottom up” by optimizing stability of sensory input in a learning hierarchy (Wyss et al., 2006) but also “top down” by optimizing predictions of the sensory consequences of actions. Following sensorimotor optimization, action effects are more predictable than when using sensory data alone (Weiller, Martin, et al., 2010).

A unified sensorimotor state space derived from both sensory and motor processes may serve as a computational basis for embodied theories of action planning (Weiller, Lär, Engel, & König, 2010). The psychological theory of event-coding finds that perception and action are processed in a common space of action and perception (Hommel, Müsseler, Aschersleben, & Prinz, 2001). Microstimulation of motor neurons at behavioural timescales (i.e. longer than usual)²⁰ elicits full behavioural patterns rather than individual muscle responses, suggesting that neurons in motor cortex do not operate by coding instructions for individual muscles but complete behaviourally relevant patterns such as grasping. This has been taken as a confirmation of the anticipation of perceptual end-positions in a perceptual space (Graziano, Patel, & Taylor, 2004; Graziano, 2006; Meier, Aflalo, Kastner, & Graziano, 2008)²¹ in inverse and forward models of action planning that close the sensorimotor loop (e.g. Novick & Vaadia, 2011; Shadmehr, Smith, & Krakauer, 2010). The concept of predictability - optimizing the predictions of action effects – may serve as an unsupervised computational scheme to extract such sensorimotor contingencies from sensorimotor space (Clark, 2012; Friston, 2010).

3.3.1.3.3 Intrinsic Motivation to Predict

However, learning to predict may not be sufficient to explain why sensory development requires active self-exploration. If the only computational objective of self-exploration would be to maximize predictions, the organism would quickly avoid the unknown unpredictable aspects of its environment. For instance, visual stimulation is optimally predictable when the organisms simply remain still in a dark room with eyes closed, but behavioural data on sensory development, prism adaption and sensory substitution argues that self-exploration behaviour samples the space of

²⁰ However, a critique of Graziano’s conclusion has been that longer stimulation times may in fact elicit neuronal networks rather than single cells, rendering the derived statements about single cell coding invalid. Graziano stimulated with impulse lengths of 500ms, while traditional microstimulation operates in the order of milliseconds, hence a functional organization of the motor cortex may be established only at the network level. I am thankful to Julius Verrel for pointing this out.

²¹ But also explicitly separate cortical structures for action and perception in the cortex have been found (Schwartz et al., 2004).

possibilities. Hence predictive mechanisms have been extended with unsupervised mechanisms that optimize the progress of how the organism learns to predict as a higher-level objective. Optimizing the learning progress leads to an intrinsic drive to select among novel situations for those that are neither fully unpredictable nor predictable and thus allow further development. Such unsupervised sensorimotor schemes have been developed in robotics and may form a computational basis for the psychological concept of intrinsic motivation (Oudeyer, Kaplan, & Hafner, 2007). Intrinsic motivation in this sense may illustrate unsupervised higher-order sensorimotor objectives of that form a top-down guidance of behaviour via emotion and motivation. Prior to explicit tasks, what may motivate the brain is to learn to predict the consequences of its actions. If this is true, sensory development is in part emotional and or motivational.

3.3.1.3.4 Reafferents and Forward Models

Physiological experiments show that predictions about action consequences (also called forward models in the literature) are generated in motor areas of cortex and cerebellum and allow the system to distinguish self-generated sensory changes from external changes via top-down refferent signals (Blakemore, Frith, & Wolpert, 2001; Bubic, von Cramon, & Schubotz, 2010; Desmurget & Grafton, 2000). Such a disentangling of internal and external sources of sensory input is important for the interpretation of sensory stimuli, for instance to differentiate if a change of the visual scene was caused by self-movement or by movement in the world (Crapse & Sommer, 2008), in the integration of signals about space (Angelaki & Cullen, 2008), and in the control of eye movements (Gallant, Connor, & Van Essen, 1998) or grasping movements (Hoffmann, Schenck, & Möller, 2005). Use of refferent signals is a general principle in motor control (Diedrichsen, Shadmehr, & Ivry, 2010; Flash & Sejnowski, 2001; Shadmehr, Smith, & Krakauer, 2010), in language comprehension (Pickering & Garrod, 2007), in social interaction (Wilson & Knoblich, 2005). Refferents are supposed to underlie our inability to tickle ourselves (Blakemore, Wolpert, & Frith, 1998) and of the development of a self (Gallagher, 2000). Disturbances of forward predictions have been suggested in a variety of sensorimotor disorders such as phantom limbs, delusions of control & agency (Blakemore et al., 2001; Roskies, 2010; Synofzik, Thier, Leube, Schlotterbeck, & Lindner, 2010) or schizophrenia (Blakemore, Wolpert, & Frith, 2002). Updating forward models is crucial to stabilize and adapt action predictions (Synofzik, Lindner, & Thier, 2008), may help in treatment of the pathologies (Ramachandran, Rogers-Ramachandran, & Cobb, 1995), and is important for the calibration both of idiothetic and allothetic space as well as the ability to locate oneself in space (Whishaw & Brooks, 1999). Hence refferent signals are foundational to many actions and perceptions in interacting with a world.

3.3.1.3.5 Higher-Level and Motor Areas vs. Lower Level Areas in Perception

Motor processes in perception have recently led to a discussion on the distinction between low- and high level areas of perception. Although primary areas are extensively studied, a direct role of the activity in primary areas or of the feed forward sweep of signals from primary into higher-level areas for perceptual awareness is highly controversial, as activity in primary areas is immensely shaped by the massive recurrent connections from higher level visual areas (Tong, 2003; Fiser et al., 2004; Olshausen & Field, 2005). In contrast, studies on binocular rivalry and perceptual category learning have suggested that higher-level areas are direct correlates of

perceptual awareness. Increases in perceptual sensitivity in visual category learning correlate directly with the learning of discriminative features in inferior temporal cortex but not with activity in early visual areas (Sigala & Logothetis, 2002). Similarly, while low-level areas do reflect perceptual processes in binocular rivalry (Wunderlich et al., 2005; Tong et al., 2006), in other experiments the alternations in subjective perception correlate strongest with activity in higher-level areas (Leopold & Logothetis, 1999). Further, certain cases of experiential blindness after restoration of retinal signalling have been interpreted to originate not from absence of visual sensations²² but from a lack of functional sensorimotor integration of sensory signals (Noë, 2004).

In this picture, perception is a holistic activity in which central and motor programming areas that integrate sensory with non-sensory information may initiate reorganization of activity in many levels of the visual system (Leopold & Logothetis, 1999). Hence, top-down influences on perception may be conceived of as a special type of predictive behaviour related to attention, ‘active sensing’, aiming for a change in perception to guide perceptual organization (Ballard, 2009; Leopold & Logothetis, 1999).

3.3.2 Visual-Spatial Attention of Acting Agents

3.3.2.1 Premotor Theory of (Visual) Attention

Also attention has recently been explicitly linked to motor behaviour. The “premotor theory of attention” grounds covert attention in a minimal form of action, such that attention is thought of as a motor intention whose action effect is not a change in sensory input as such but a modulation of processing at the attended location (for a review see Rizzolatti & Craighero, 2010)²³. A number of studies suggest to describe shifts in visual attention during fixation as planned saccades that are not executed. Neuroimaging results show that visual attention shares cortical networks with the eye movement system. Directing attention towards a location activates the ocular motor system even if no movement is required. And in some experiments, when the eyes could not move to a certain location, neither could visual attention. Further, direct microstimulation of the frontal eye fields, a primary motor area for eye-movement control, modulates both spatial attention as well as gain factors in higher-level visual areas, leading to enhanced processing of the intended location.

²² Although it is not clear in Noë’s writing whether visual sensations refer to pure visual signals or entail some form of basic visual awareness, the more general valid point is the observation that visual signals seem to require sensorimotor integration for normal visual perception. I am thankful to Mike Beaton for discussing this.

²³ A tight interdependency between motor behavior and the ontogenetic development of perceptual processing and attention has already been noted in Ulric Neisser’s classic text book on cognitive psychology (Gyr, Brown, Willey, & Zivian, 1966; in Neisser, 1967), albeit not further explored.

3.3.2.2 A Sensorimotor Account of Visual Saliency

The argumentation so far should not be taken to question a contribution of salient visual features to visual attention in principle. Rather, models and experiments above (and below) suggest an embodied reframing of the saliency model. The original saliency model adheres to the (input part of) the input-output sandwich that has been associated with artificial intelligence (Hurley, 1998). Sensory processing forms a suitable input representation (the saliency map) in a pre-attentive processing step (Tatler et al., 2011). On the basis of which a minimal stage in the form of a winner-takes-all decision rule instructs a subsequent shift of attention or a subsequent motor orientation towards a region of space. While the original saliency model can be sandwiched within a sensorimotor loop, it does neither consider the motor system nor cognition as constitutive part of the attention model per se (section 3.2.3 above).

By contrast, a premotor model of visual attention suggests a constitutive role of (whole-body) motor processes both in the definition of salient features and in the decision processes that guide attention. In goal-directed natural movement, gaze is adjusted by movement of the head and torso in addition to movements of the eyes. If the respective motor idiosyncrasies play a constitutive role also in a pre-motor theory of visual attention, saliency-based models need to be modified beyond an obvious increase of the degrees of freedom for the adjustment of gaze provided by the additional movements of head and body. First, in basic motor control it has been suggested that individual effectors are not defined and controlled by the nervous system in structural/anatomical but in context-dependent functional terms of a respective motor activity as a whole (Graziano, 2006). Thus basic motor control suggests a role of pre-motor processes depending on individual functional actions of the entire body for a premotor theory of attention as well. These mechanisms for instance likely include individual spatial coordinate transformations (Salinas & Abbott, 2001; Snyder, 2000; see also the next paragraph) and challenge the retinotopic reference frame implied by typical saliency model and suggest functional or even situation-dependent frames of references. Second, at the systems level, motor behaviour is goal-directed in the service of tasks. In consequence, visual attention has been conceptualized as a motoric way of intending an engagement with the world in an orienting response of the body to functional points of action that are not yet observable in movement (Hayhoe & Ballard, 2005; Hayhoe & Rothkopf, 2011). Taken together, two acts of shifting (covert) visual attention or gaze to a point in space might be realized via different motor-processes when performed within different functional motor contexts and with different effectors, leading to distinctive internal dynamics of the two attention shifts despite the common reference point in and thus a common bottom-up saliency of the world. Third, as a consequence, the feature space for saliency may turn out to be of sensorimotor rather than exclusively sensory nature. In this scheme, salient features would mark invariances in the sensorimotor space that are informative for action. From an optimal coding point of view, sensorimotor aspects are an extension to bottom-up feed forward influence as in the classical saliency model, rather than an exclusion thereof. Normative principles are likely to establish an automatic assignment of saliency to sensorimotor discriminations that are most useful in a

statistical sense over the broad variety of natural behaviour²⁴. The contribution of the respective sources to a sensorimotor salience model at a systems level is an interesting question on embodied perception and attention not addressed in the original salience models or in typical laboratory eye-tracking paradigms. This highlights the potential of experiments in natural settings to trigger and identify the complexities of a sensorimotor attention system that is fine-tuned to natural behaviours.

3.3.2.3 Embodied Spatial Processing In a Three-Dimensional Action Space

A most important aspect of sensorimotor processes is the coordination of the respective reference frames of body parts and action points in the world. Spatial reference frames and spatial processing also develop by activity-driven principles in embodied interaction with environments. While at the level of the body, spatial idiothetic reference frames are hard-wired in the biology of the muscles and effectors as well as the sense organs, the neuronal representations of idiothetic frames at later stages are re-learned by plastic learning. For instance retinotopy, the spatial reference frame of the retina, is not preserved anatomically by a precise retinotopic mapping to cortical areas but lost in the optic nerve and then re-established in self-organization processes on the basis of spatial correlations in visual input (Chklovskii & Koulakov, 2004). Similarly, although it is not entirely clear how much of the processing machinery for allocentric reference frames is hard-wired, allothetic representations such as hippocampal place, grid and head direction cells can be learned on the basis of the sensory signals (Franzius, Sprekeler, & Wiskott, 2007; Wyss, König, & Verschure, 2006) and actions (Weiller, Martin, Dähne, Engel, & König, 2010) of a moving agent. Compatible with this, crawling behaviour affords active exploration and a new ecological perspective of the world to the infant, which are both important in the formation of cross-cortical connections and the development of the hippocampus, which is important in allocentric processing (Bell & Fox, 1996). Further, spatial processing is essentially a multimodal process, with a crucial role of vestibular sensorimotor contingencies (Angelaki & Cullen, 2008). Adding vestibular sensation to the acting agent in the above learning models allows the system to differentiate frames for the position (place cells) and the direction of the head (head direction cells) (Franzius et al., 2007). And again, active exploration is necessary, for instance for the calibration of the multimodal idiothetic and allothetic sources of spatial signals (Whishaw & Brooks, 1999).

Once spatial reference frames are established, maintaining spatial consistency and stability in the dynamic flow of sensory and motor signals is a major challenge for behaving nervous systems (Noë, 2002). The retinotopic input from the retina changes substantially with every movement of the eyes, but unnoticed in our perception, which is stable over time. Forward mechanisms support spatial consistency by gaze-centred remapping of target locations across saccades during saccadic eye-movements already in retinotopic coordinates (Medendorp, 2011). However, spatiotopic transformation is supposedly relatively slow compared to the speed of saccadic eye-movements, necessitating further stabilization mechanisms. Spatiotopic stabilization is aided by transient mechanisms around the time of the saccade. For instance, selective suppression of motion-properties of the stimulus reduces the perception of saccade elicited motion.

²⁴ Konrad Körding, in personal communication at the workshop “Neural Coding, Decision Making & Integration in Time“, 2012.

Location shifts in dependence of saccade direction or by compression of space around the saccade support trans-saccadic alignment of stimuli patches (Burr & Morrone, 2011). Yet the complexity of the stability problem increases with the degrees of freedom provided by additional movement of head and body. In addition to eye-proprioceptive input, further input from other body parts such as neck-proprioceptive input provide massive signals for spatial processing and attention (Gramann, Gwin, Bigdely-Shamlo, Ferris, & Makeig, 2010), which also play an important role in achieving stability. Given that the extended oculo-motor system coordinates movements of gaze by movement of eyes, head and body, it is likely that visual consistency and stability rely on sensory feedback and efference copies from the whole body. A recent review, on which this paragraph relies, concludes that three-dimensional action space is “an evolving representation whose internal metric is updated in a non-linear way, by optimally integrating noisy and ambiguous afferent and efferent signals” (Medendorp, 2011). Given a premotor theory of attention and a general principle of circuit sharing (section 3.3.4), this characterization is likely to transfer to visual-spatial attention as well.

3.3.3 Spontaneous Attention²⁵

Following phenomenology, the consideration of selective attention so far has not addressed another aspect of the nature of attention: spontaneous attention (for a review see Cosmelli, 2009). Already William James was aware that spontaneous and transitive shifts of attention directed to internal rather than external events in the stream of consciousness are overabundant in everyday life (e.g. Smallwood & Schooler, 2006). This spontaneous aspect of attention seems vital in natural behaviour and understanding it may shed important insights on the nature of attention in general. Spontaneous attention has been (and is) difficult to systematically examine for reasons related to experimental design, and neuroscience has only very recently begun to address spontaneous shifts of attention in paradigms on stimulus-independent day-dreaming and mind-wandering (e.g. Christoff, Gordon, Smallwood, Smith, & Schooler, 2009). First studies could link some aspects of spontaneous attention to the supposedly spontaneous activity of stimulus independent components of so called default networks in the brain. However, these studies also suffer from ecological irrelevance as spontaneous attention usually occurs in the context of the complex situations of everyday life. Alternative experimental strategies provide experiments in rich and varied environments with several tasks from which the subject can spontaneously choose, paired with markers of the concrete behaviour chosen individually (Cosmelli, 2009). Gaze movements are markers of externally directed attention that are easy to register. Gaze movements in social interaction in real world scenes offers such a variety of tasks on the basis of a multiplicity of bodily cues available to the subject (Smilek, Birmingham, Cameron, Bischof, & Kingstone, 2006). Gaze movements have also been used as a potential marker of free attention in laboratory studies on free viewing behaviour (Reinagel & Zador, 1999). Again, measuring shifts of gaze in whole body movements within natural environments that offer a variety of spontaneous behavioural options is also a promising paradigm for the study of spontaneous attention in the absence of laboratory restrictions. A larger description of this methodology is given in section 3.3.5.

3.3.4 Circuit Sharing in the Sensorimotor System: Embodiment of Higher-Level Concepts, Social Interaction and Language

Since Yarbus (1967) realized the role of eye movements in cognition, their relation to higher-level processes such as planning, problem solving, memory or social interaction has been a major source for the saying that eye-movements are “a window to the mind” (section 3.2.3). Within the embodied turn the sensorimotor loop has been implicated in higher-level cognition in all major fields ranging from artificial intelligence to cognitive psychology and linguistics, mainly in attempts to provide symbol grounding (Anderson, 2003; Clancey, 1997; Clark, 1997; Sheets-Johnstone, 1990). Hence embodied grounding of higher-level cognition is likely to provide architectures that are informative for the control of eye-movement in natural cognition as well (Ballard, Hayhoe, Pook, & Rao, 1997; Hayhoe & Ballard, 2005; Hayhoe & Rothkopf, 2011).

²⁵ I am thankful to Evan Thompson for pointing me towards the work of Diego Cosmelli about this important aspect of attention (Cosmelli, 2009).

New, or behavioural, artificial intelligence (AI) attempts to derive physical grounding of cognition via subsumption architectures of independent, de-centralised and domain specific sensorimotor processes. Behavioural AI spells out symbols in terms of behavioural affordances and the sensorimotor discriminations necessary to perform the related actions rather than in terms of objective representations and their formally semantic truth relations to the state of affairs in the world (Brooks, 1991)²⁶. Outside behavioural robotics, new AI also on theoretical grounds described higher-level abilities such as categorisation or declarative memory as sensorimotor processes (Clancey, 1997; Winograd & Flores, 1986).

3.3.4.1 Sensorimotor Metaphors in Language

At the centre of Lakoff & Johnson's influential program of an embodied linguistics is the idea of cross-domain mappings between sensorimotor and conceptual domains. Everyday language heavily adopts metaphorical usage of spatial sensorimotor concepts, and Lakoff & Johnson were among the first to hypothesize that this is not only a manner of speaking but may reflect the underlying architecture of the conceptual system. If everyday sensorimotor praxis gives meaning to our understanding of the world, our general inferential systems should make use of knowledge about sensorimotor practices as well (Anderson, 2003; Johnson, 1980). Further, from a language-action perspective, language itself is a skilled action that maps back to the sensorimotor system and organizes sensorimotor processes by means of conceptualization (Clancey, 1997).

3.3.4.2 Memory as Categorizing the Sensorimotor Space

A sensorimotor conceptualization also drives Glenberg's (1997) skill-based re-formulation of (declarative) memory that gained influence in cognitive psychology. In his view, memory developed not for memorization of declarative facts but to aid categorizations in the sensorimotor system that "mesh" constraints given by the body and the situation in categorical actions. While Glenberg erroneously seems to assert to the cognitivist notion that categorization would have to occur in symbolic format, the novel terminology of "meshing" clearly is reminiscent to recent machine learning approaches for learning and clustering in the sensorimotor space.

3.3.4.3 The Perceptual Symbol Hypothesis

Borrowing from Newell and Simon's metaphor of the Physical Symbol Hypothesis, Barsalou phrased a Perceptual Symbol Hypothesis (Barsalou, 1999, 2008, 2010) as a guideline for sensorimotor research on higher-level concepts. Drawing in part on the above role of feedback from motor areas for object perception (section 3.3.1.3), he suggests that concepts are created by re-activation of (multi-) modal lower-level sensory areas from higher-level motor areas. The perceptual symbol hypothesis is intended to spur research on the phenomena cognitivism classically described as propositions, declarative memory or productivity via simulations of sensorimotor processes (a form of prediction).

Neuroscientific evidence for sensorimotor grounding of higher level processes accumulated vastly within the last decade (Barsalou, 2010) and can not be reviewed here beyond

some representative studies. Imaging studies in language comprehension could relate semantic networks that are active when understanding a word to the sensorimotor circuits of the physical object or action to which the word refers to, for instance to body parts performing an action, to the form and colour of typical objects involved, or to their touch properties (Just, Cherkassky, Aryal, & Mitchell, 2010; Pulvermüller & Fadiga, 2010). While much of this work is informal or demonstrational, computational neuroscience has begun to move towards predictive modelling of higher-level processes in sensorimotor terms (Pezzulo et al., 2011). Recently, machine learning started to build computational models for neuronal activity, and found that observing the neuronal activity of a set of sensorimotor words predicts the neuronal activation to unseen words much better than do abstract predictor words. This led to the conclusion that “concrete nouns in part are grounded in sensory-motor features” (Mitchell et al., 2008). On this basis, neuro-semantic approaches are pushing the field of embodied language understanding from a pre-theoretical stage towards computational modelling. This exciting approach may yield a data-driven method of integrating neuronal semantics, understood in terms of motor aspects, and linguistic semantics, understood e.g. in terms of word co-occurrence frequencies in spoken language, for the sensorimotor analysis of higher-level concepts (Just et al., 2010).

3.3.4.4 Circuit Sharing and Connectivity Analysis

Meta-analysis of common brain areas that are co-active over a broad variety of domains from perception and attention to action and language not only argues for a sharing of neuronal circuits but also for the redeployment of existing pathways when novel functions develop ontogenetically or phylogenetically (Anderson, 2008, 2010). In consequence, higher-level tasks such as language seem more widely distributed over the cortex than the processes of perception and action that develop earlier. This analysis suggests that brain organisation may be neither modular in a cognitivist sense, nor holistic, but hierarchical. Increasingly graph theoretic methods prove promising in identifying information flow, size, or connectedness between hierarchies in both real and modelled sensorimotor networks (Kaiser, Hilgetag, & Kötter, 2010; Lungarella & Sporns, 2006; Sporns, 2011; Zhou, Zemanová, Zamora, Hilgetag, & Kurths, 2006).

3.3.5 Free Spontaneous Behaviour and Natural Data Recording - Methodologies for Ecological Neuroscience

“A process cannot be understood by stopping it. Understanding must move with the flow of the process, must join and flow with it”.
- Frank Herbert, *Dune (First Law of Mentat)*

If the brain organises dynamic action in complex sensorimotor loops within natural environments, and is shaped by activity-dependent plasticity a result thereof, methods of investigating the brain in consequence benefit from complementing controlled laboratory experiments with real-world strategies that sufficiently approximate natural complexity. One novel strategy extends the natural stimulus approach (section 3.3.1) to the temporal structure of natural stimuli. This approach has been applied in recent physiological recordings of brain dynamics in the presence of the spatio-temporal information in natural movies (Einhäuser & König, 2010; Kayser, 2004; Olshausen & Field, 2005; Onat, König, & Jancke, 2011), aided by the development of massively parallel recording of large-scale brain activity (Kording, 2011; Stevenson & Kording, 2011).

The present thesis implements a second strategy for sensorimotor research on visual attention: the analysis of natural behaviour in spontaneously chosen tasks within real-world contexts. There are a number of recent examples of this general approach. Multichannel mobile brain imaging systems (MoBi) register mobile recordings of EEG together with body movements, auditory and visual scene to examine the links between distributed brain systems and motivated natural behaviour (Makeig, Gramann, Jung, Sejnowski, & Poizner, 2009). Systems for monitoring natural speech and behaviour track child language development, for instance to relate the ontogenetic onset of individual word usage to necessary prior sensorimotor experiences (Lazer et al., 2009; Roy, 2005). Electronic second skin attempts everyday tracking of physiological markers of the body (Ma, 2011), and mobile miniature positron-emission-topography (PET) systems (RatCap) move brain imaging towards the simultaneous assessment of rodent behaviour and molecular neurochemistry (Schulz et al., 2011). Mobile eye-tracking has been used to study eye-movement behaviour in freely moving and socially housed monkeys to investigate the interaction of sensory, motor, motivational and social aspects of eye-movements (Shepherd, Deaner, & Platt, 2006; Shepherd & Platt, 2006).

Experimental designs in these scenarios make use of subjects that are less restrained to allow for free behaviour with self-generated, spontaneously motivated tasks. They grant sufficient liberty so that natural mechanisms of cognition can play out under the multiplicity of external and internal processes of the organism (Engel, 2011).

When behavioural variables are not known and in consequence not operationalized in full detail in advance, studying spontaneous behaviour also poses novel demands on data analysis that complement classic a priori hypothesis testing. Machine learning approaches allow post-hoc pattern identification within massive amounts of multi-channel data (Buzsáki, 2004; Kording, 2011; Mitchell, 2009; Reed & Kaas, 2010), or the assessment of connectivity in the sensorimotor information flow and neuronal pathways (Lungarella & Sporns, 2006; Sporns, 2011). Recent advances in statistics complement linear dependency measures such as correlation with nonlinear

information theoretic dependency measures based on mutual information (Reshef et al., 2011). Novel event-based techniques may be able to analyse spontaneous behaviour on the basis of low-frequency, or even single-trial events (Churchland, Yu, Sahani, & Shenoy, 2007; Cosmelli, 2009; Debener, Ullsperger, Siegel, & Engel, 2007; Mazaika, 2007; Müller et al., 2008). Finally, neurophenomenological approaches have the potential to revive first-person introspection as a data source. First- or second person descriptions of trained observers during behaviour have already been taken as informative subjective markers for post-hoc categorization of spontaneous events that can feed into physiological data analysis (Lutz, Lachaux, Martinerie, & Varela, 2002), and this strategy might eventually be developed into a novel form of higher-level psychophysics (see section 6.2.9) that allows relating internal markers of conceptual, emotional or motivational processes to physiological and behavioural records of natural behaviour.

3.3.6 Intermediate Summary

This section summarises the signal processing approach to embodiment presented so far. It suggests a sensorimotor account of visual salience and attention and motivates gaze-tracking research in the real world under natural whole-body activity.

Neuroscience developed its roots in signal processing (Barlow, 1961) and begins to shift of the role of feedback loops back into focus in a renaissance of pragmatic philosophical thinking in cognitive science (e.g. O'Regan & Noë, 2001). In general, the resulting framework shapes a representational approach, yet in sensorimotor rather than abstract truth-functional terms:

- Minds, brains and cognition organize embodied action within a world.
- Ecological and bodily contexts are part of the object of analysis, that is, part of the computational and explanatory loops. Cognition manipulates the action-oriented structuring of the concrete sensorimotor system that is adapting to the world.
- Abstract representations are thought of as high-level sensorimotor representations, such that cognition does not manipulate abstract formal representations of the world that are independent of the sensorimotor context, and internal processing is highly context-sensitive and domain specific. On the other hand, a normative goal of sensorimotor cognition is to develop more abstract forms of clustering, such as hierarchical sensorimotor contingencies. There is hope to eventually spell out Barlow's vision that symbols are an abstract form of signal processing in sensorimotor terms (König & Krüger, 2006) resulting from the activity in the sensorimotor space.
- Research emphasizes how concrete internal processing is a consequence of the (statistical) structure in the ecological world, the physiology of the agent's sense organs, and the intentional actions of the organism. These aspects are interrelated in that activity-based sensory clustering of the sensorimotor space is, among other things, a basis for more complex behaviour and thereby creates novel sensorimotor contingencies that in turn feed back into sensation. There is a general interest on how a more abstract internal processing develops from concrete processing over time by the reuse of neuronal structures.
- Pragmatic sensorimotor paradigms seem to reject the cognitivist notion that conceptual knowledge is different in principle from know-how and sensorimotor skills. Higher-level processes of memory and categorization are approached conceptually and experimentally in terms of their role in sensorimotor couplings. From a more cognitivist point of view, the distinction remains important however, and it is an empirical question to what degree also sensorimotor accounts of abstract concepts will require cognitivistic elements for instance of categorization.
- Experimental settings make use of spontaneous behaviour to elicit the multitude of naturally interdependent processes.
- The temporal nature of the situation suggests a temporal organization of brain and mind. This temporal aspect should play a foundational role in models and experiments. Novel methods of data recording aim to co-register cognition and neuronal activity in relation to the functional aspects of a situational unfolding rather than in relation to stimuli in isolation.

- The complexity involved in operationalizing spontaneous behaviour in natural situations necessitates complementary data-driven strategies for data analysis, for instance involving machine learning, information theory or Bayesian approaches and somewhat restricts the possibilities for classical hypothesis generation and testing.

With respect to perception and attention, the analysis suggests that:

- It is an empirical matter to which sensory features the brain responds to, dependent on the sensorimotor signal statistics of the behaving agent in the natural world and the physiology for plastic learning provided by evolution. Processes of sensory plasticity are better described as a special case of sensorimotor plasticity. Sensory signal processing principles such as optimal coding are better understood as a special case of sensorimotor coding schemes. Hence, sensory features are likely a sensorimotor rather than a purely sensory property. In consequence, visual salience is likely to single out features in the visual sensorimotor space rather than the purely sensory visual space.
- Attention, perception and spatial processing involve a large number of re-afferent signals and should be thought of as a consequence of sensorimotor processes that couple with the world. Relevant sensorimotor processes include intentional goal-directed action (higher-level cognition) as well as perceptual sensorimotor goals such as image stabilization, spatial consistency, three-dimensional vision or perceptual organization.
- Directing gaze is a whole-body process within the world rather than a function of eye-movements within head-coordinates. This implies that other body parts that aid the orientation in space, such as torso, shoulder or hips need to be coordinated to direct gaze, introducing various forms of coordinate transformations and other embodied constraints to the control of gaze-movements.
- Attention, perception and spatial processing are inherently temporal phenomena. Their temporal characteristics should be explicitly considered in models and experiments.
- Gaze-movements play a constitutive role in a broad variety of aspects of everyday behaviour that go beyond the selection of salient information from a visual display. Examples are whole-body orientation, hand and tool use, aspects of higher-level cognition as well as social interaction. Thus, eye-movements are a window into natural cognition and reflect many processes of embodied life, which models and tests should consider.
- Visual salience in a sensorimotor space might entail discriminative features that relate to prior hypothesis about the possible unfolding of actions given the current situation and goals.
- The methodological challenge of embodied neuroscience naturally applies to vision and attention: how to obtain data of the real visual processes at work. This somewhat restricts the methodology of artificial laboratory experiments on isolated components. The current thesis takes a complementary methodology and records massive amounts of data in natural visual behaviour in an unobtrusive way. This allows the natural processes to play their role and is a prerequisite for their identification and examination.
- Generally, analysis will rely on machine learning to find patterns that link visual input and behaviour but are likely unknown in advance or merely hinted at. In this sense, pragmatic

visual neuroscience in natural settings is a call to extract hypotheses from large datasets themselves (given the assumptions of the particular machine learning framework).

In sum, the presented approach provides elements for an information theoretic computational and experimental implementation of Dewey's or Merleau-Ponty's notion that perception originates in action.

3.4 Enactive Cognition and Perception

The next section briefly sketches a non-representational alternative strand of embodiment. The enactive approach to cognition has roots in part in the early physiological work of Maturana and Lettvin (Lettvin et al., 1959) as well as in second-order cybernetic constructivism (Di Paolo, Rohde, & Jaegher, 2010; Froese, 2011; Thompson, 2004; Varela et al., 1991), the biology of life (Maturana & Varela, 1992) and in hermeneutical philosophy (Morley & Hunt, 2000). It argues that genuine cognition and meaning are constructed or enacted in activity without representation.

3.4.1 Enactive Metaphysics: Neuro-Hermeneutics, Constructivism and Holistic Top-Down Causation

Enactivism may be seen as a radical alternative to cognitivism and traditional embodiment due to the alternate metaphysical core of the program (Di Paolo et al., 2010; Schumann, 2004). In broad summary, the enactive program attempts an analysis of cognition in an appraisal of relational processes of structural coupling that can form genuine, self-constituting cognitive identities that normatively constrain their individual parts. A main motivation is that structures that constitute themselves in their own activity may have genuine purpose *for themselves* in the inner perspective of the system, as opposed to a representation of meaning that is assigned from an outside observer or scientific theory. Thus at its core enactive theory is a take on intentionality and sets out for a naturalization of genuine meaning in a physical world. In some sense enactivism thereby revives the cognitivist idea of genuine artificial intelligence that has been part of strong semantic information processing, yet without the notion of information and representation (Lasse Scherfig, personal communication, 2012). In contrast to artificial intelligence, enactivism originates in the biology of life, and from this basis challenges classical views on what counts as a system but instead explicates biological ways of system formation. Neither world nor body are taken as given, neither as clearly identifiable parts of the natural world nor as objects of scientific analysis, but rather are taken as interrelated aspects of an on-going co-creation of what is system and what environment. The driving intuition is that once a science of cognition can explicate how system and context are established in activity, a genuine explanation of meaning and cognition and the interrelated aspect of what is life follows from there.

Following the enactive take on embodiment, the representational embodiment work of above attempts a non-syntactic dynamical reformulation of functionalism, partly because it includes aspects of the body and the situation only as context for extended computational-representational engines or minds (Clark, 2006; Di Paolo et al., 2010). Partly also because representational embodiment shares the cognitivist metaphysics of teleological mapping between a meaningful world and brain mechanisms and thus likewise can not address the problem of grounding in a fundamental way as it does not address how system and world and value and meaning originate interdependently (Stewart et al., 2011).

The contrast between enactivism and representational embodiment / cognitivism reflects a major division in philosophy between two broad classes of approaches to knowledge and inquiry: the analytic and the hermeneutic tradition (Morley & Hunt, 2000). Section 3.1 argued that the natural sciences in general and cognitivism in particular follow the analytical strategy that seeks to

find a set of elements and rules that can fully describe a situation without further context. Enactivism, albeit also aiming for lawful explanations, does not follow the general analytic approach. By contrast, it views the analytic focus on the delineation of system and environment liable to miss the conceptualization of identity creation in relational processes that are inseparable (Di Paolo & Iizuka, 2008). In this sense, enactive thinking follows that general approach of hermeneutics. Thus the program of enactivism is closer to continental philosophy and phenomenologists such as Heidegger, Husserl and Merleau-Ponty, the late work of Wittgenstein and to second-order cybernetics than to the analytic tradition in the metaphysics of logic, cognitivism or the early work of Wittgenstein (Morley & Hunt, 2000). The wish for a naturalization of hermeneutics is clear in the term “neuro-hermeneutics” Varela used prior to the terms “enactivism” and “neuro-phenomenology” (Varela et al., 1991). Yet unlike the philosophical foundation, enactivism aims for naturalization in “precise, operational, albeit non-functionalist” theory (Di Paolo, 2008). Central to the strategy of naturalization is a focus on mechanisms of top-down causation (Thompson & Varela, 2001; Thompson, 2007) that allow autonomous identities to set their own normative laws while obeying the laws of physics (Di Paolo & Iizuka, 2008). The notion of self-constituted normativity formalizes two central hermeneutical tents: the creation of objects in the interaction of the system as a whole and the importance of the history of this activity for the constitution of the system (Morley & Hunt, 2000).

3.4.2 Autopoiesis, Autonomy, Adaption, Intrinsic Teleology, and Meaning Creation through Sense-Making

Maturana and Varela historically formulated enactivism to bootstrap cognition from the dynamical processes that create systems and boundaries they had established in their work on the biology of life (Froese & Stewart, 2010). In the centre lies the concept of autopoiesis: the idea of networks of closed metabolic feedback loops that refer back only to processes within themselves and thereby self-produce and maintain their own identity as a system. Autopoiesis offers an explanation of cells as a basic form of a living, self-sustaining dynamic identity. A foundation of enactivism was in the application of autopoiesis idea also to a biological explanation of cognition (Maturana & Varela, 1992).

Recent extensions generalize autopoiesis to the concept of autonomy. One aspect is that a system can be autonomous without being autopoietic in a metabolic sense. Broadly speaking, a system is autonomous if it follows laws established by its own activity that have become normative constraints for further existence of the system. This requires the self-generation of the system as a distinct identity that follows laws given by its own constitution rather than by external design. An identity, metabolic or non-metabolic, is created if a network of processes is operationally closed, i.e. if the system’s enabling conditions in part always refer to other processes within the system such that an identifiable unity can be defined, and if the system operates to adaptively maintain its own autonomy under environmental pressure (Di Paolo & Iizuka, 2008; Di Paolo et al., 2010).

Autonomy and adaption have been taken as foundations for systems with intrinsic teleology (Di Paolo, 2006). Enactivism spells out a genuinely meaningful perspective on the world *for the system* in reference to the norms established under the maintenance of the systems’ autonomy under pressure, a process dubbed as sense-making (Di Paolo et al., 2010; Thompson, 2007; Varela et al., 1991).

3.4.3 Mind-Life Continuity

Since the conceptual tools of autonomous identities, adaptation and sense-making, are based in the biology of life, they have been taken to imply a continuity between the domains of cognition and life. Hence enactive analysis has been applied to many aspects of living organisms such as their metabolism, the immune system, the nervous system or social groups (Varela, 1979). The mind-life continuity hypothesis argues that these levels are in principle inseparable once they emerge, since sense-making processes occur in relation to autonomous processes that are constituted across levels of analysis (Froese & Paolo, Di, 2011). To give an example, enactivists argue that cognition-as-sense-making provides a value basis for emotional valence, which co-constitutes intentional behaviour, which co-constitutes personal identities and social-worlds. Given that the sense-making behaviour is taken to occur at the metabolic, bodily, emotional and social levels at once, and that autonomy entails operational closure, also cognition, emotion and the social fundamentally integrated rather than modular aspects of neuronal, metabolic and psychological processes of sense-making (e.g. Colombetti, 2010; Colombetti & Thompson, 2007). The mind-life continuity hypothesis challenges the functionalist explanations in the programs of cognitivist / embodied / or extended minds that describe the living system only as a contingent substrate of the functionalistic level of cognition. From the argument that functionalism can not explain autonomy, it can not explain cognition as well (Froese, 2012). If processes of autonomy and cognition-as-sense-making are mutually constitutive, they cannot be separated for analysis, which explains why a functionalist explanation of intentionality in cognitivism or representational embodiment must fail (Di Paolo, 2008)²⁷. Instead, processes of a living body are required as an originating source of autonomous organization and cognition (for a discussion see Thompson & Stapleton, 2008).

On the other hand the enactive approach does not necessarily constrain processes of life to biology but explicitly adheres to the possibility of artificial life (Froese & Ziemke, 2009; Thompson, 1997).

3.4.4 Computational Implementations of Enactivism

Enactivism seeks operational explanations, and mathematical and computational modelling remains a crucial tool at hand. The initial publication of the enactive paradigm discussed self-organisation schemes such as cellular automata, genetic algorithms, and connectionist models (Varela et al., 1991). In his later life Varela started to approach enactivism with the tools of complex systems theory (Froese & Stewart, 2010). Since then in particular the complex and adaptive systems group at the University of Sussex has approached enactive processes with the methodology of evolutionary modelling of minimal control architectures (Harvey, Di Paolo, Wood, Quinn, & Tuci, 2005). Enactive theory poses novel constraints to models of cognition in the modelling of conditions for evolutionary development. Enactivism argues that models can only instantiate cognition if they are autonomous, and that in consequence, artificial models of cognition cannot be fully set up by a designer. At some level, processes of cognition must define their *own* constituency in laws established in their own activity also in the

²⁷ I am thankful to Tom Froese and Miriam Kyselo for pointing me to the literature on contrasting functionalism and enactivism.

model, otherwise they will not meet the autonomy requirement (Di Paolo & Iizuka, 2008; Froese & Ziemke, 2009). Thus a major motivation for evolutionary robotics is to limit the modelling of a systems by design to the modelling of developmental constraints under which autonomous systems can form in simulation, and the solutions found by artificial evolution often transgress classical system boundaries (Di Paolo & Iizuka, 2008). To give just one example, enactive evolutionary simulations can evolve systems capable of plasticity and learning in the state space of dynamical systems in the absence of plastic changes at the hardware level (Di Paolo & Iizuka, 2008). This may provide an operationalization of the hermeneutical precedence of the relational and historical level of analysis over individual structural analysis and design of a system.

Very recently the topic of computational measures for enactive analysis of physiological data has emerged. The 2011 meeting on the “Future of the Embodied Mind” intensively discussed the use of information theory and signal processing to capture enactive concepts such as autonomy, agency and adaption for instance by identification of (closed-loop) information-flow (see also Seth, 2010).

3.4.5 Enactive Perception

Enactive accounts have been among the first in cognitive science to implement the phenomenological and pragmatic traditions that see perception not as passive acts of representation but as an activity. Similar to the representational sensorimotor picture of above, much of the inspiration has come from research on sensorimotor plasticity and sensory substitution. Enactivism maintains that perceptual content is constituted by implicit sensorimotor skills in the use of the sensory consequences of movements. Yet in contrast to representational embodiment, the enactive explanatory toolkit conceptualizes sensorimotor skills in terms of autonomy and sense-making rather than in terms of embodied sensorimotor representations.

What follows is that enactivism considers it impossible to differentiate clearly between internal and external forces of perceptual couplings. Enactivism focuses on on-going functional relations also in the account of perception because “cognition is a relational phenomenon and thereby has no location” (Di Paolo, 2008). The program searching for neural correlates as necessary and sufficient conditions for the mental has mistaken this to presume that enactivism would thereby deny a causal role of neurons in perception and cognition (Koch, 2004). This is clearly an internalist overstatement of the enactive position. What is meant is that enactive feedback loops extend beyond brain, body and skull, thereby denying the internalist and often representationalist supposition that perceptual processes are exclusively internal. Yet this does not entail that enactivism embraces strong externalism instead, nor that it denies a role of neuronal processing in perception as such. A core enactivist argument is that the very division is misguided in the prior assumptions on what is internal and external (Di Paolo, 2008; Thompson & Stapleton, 2008). If top-down causation can render the whole more than the sum of its parts via the generation of its own laws, enactivism argues, the minimal supervenience base of conscious perception is not restricted to the internal neuronal stages of sensorimotor loops but in holistic processes that include the body and the world, and in inseparable, co-constituting ways (Hurley, 2006).

Enactive sense-making thereby poses a conceptual challenge for physiological work that seeks to find atomic individual properties down towards all levels of physiological analysis. In the traditional view, local neuronal modulation may be a result of local mechanisms that neurons

provide for interfacing with other neurons, such as expression or basic physiological rules for bottom-up and top-down synaptic integration (see also section 3.3.1.2). In the enactive view, relational processes of identity-formation across levels of analysis applies to neuronal activity as well, rendering an analysis of atomistic individual properties of neurons impossible without their constitutive contexts and self-generated activity laws. While the viability of the enactive approach can not be explored in this thesis, similar considerations have inspired temporal attempts to neuronal coding via synchronous cell assemblies (Engel, Fries, & Singer, 2001; Engel, 2011; Thompson & Varela, 2001). If such processes extend beyond the skull, the enactive theory in consequence requires novel physiological experiments and relational methods of data analysis within active sensorimotor loops. In this view also eye-movements may form part of the supervenience base of visual perception.

Similarly, second, the mind-life continuity hypothesis implies that the minimal supervenience base of perceptual consciousness is not exclusively related to the processes of sensory perception but requires an account of creature consciousness - the inner awareness of a living body as a self-sustaining system (Thompson, 2007). The intuition is that consciousness, including perceptual consciousness, is in essence a life-regulation process that non-trivially depends on a living body in its world (for a summary of this view see also Thompson, 2005). Perception, cognition, and action are understood as aspects of sense-making that occur at multiple levels of a living organism including its metabolism, immune systems, emotion, nervous systems or sociocultural identity. Therefore, for many enactivists it seems misleading to distinguish between higher-level and lower level perceptual areas, as perception is not a linked chain of events between areas close to sensory input and areas close to muscle output. Perception, cognition and action rather are “fused, inseparable and complementary aspects” of the agents sense-making (McGann, 2010, p.18). The important and far-reaching implication is that without a lived intentional action context and processes of adaptive sense-making, there would not be anything to perceive as such (McGann, 2010). Following Anderson’s terminology the mind and life continuity hypothesis might be seen as an argument against a hierarchical and in favour of a holistic architecture of the brain (Anderson, 2008), a debate that dates back to the early beginnings of sensory physiology (Martin, 1994). Still, an interesting question is whether hierarchical sensorimotor networks can implement the enactive theory when they include classically non-sensory-motor areas such as emotion (Thompson & Stapleton, 2008), leading to a holistic yet hierarchical architecture of the brain.

Third, enactivism challenges sensor-driven definitions of a modality and the possibility of purely uni-modal perception (McGann, 2010). Enactivism sees what we perceive as occurring within a modality not as fixed by the particular sense organs in which a given sensory signal originates. A modality rather emerges at the integrated level of perception in “areas of stability within the space of possibilities” (p.14) that are invariant over different live contexts of goal-directed sense-making processes, in part by the sets of sensorimotor skills involved. In other words what constitutes a modality in the enactive view is the specific sensorimotor activity, not the sensory source. And therefore, the usage of visual sensorimotor devices may derive vision-like perceptions from tactile signals via vision-like engagement with the world. A radical implication is that aiming for a theory of uni-modal processing may be misleading as a strategy for a general theory of perception. Even though it is useful to differentiate between visual or auditory aspects of

perception, between sense organs and between their specific sets of sensorimotor laws, the enactive prediction is that any single percept is always multi- or transmodal and never based on only visual or only auditory afferent signals (McGann, 2010).

3.4.6 Transmodal Inter-Subjective Perception

Transmodal non-verbal social experience yields a useful illustrative example for a role of the concept of sense-making and the bridging of levels of analysis in attention and perception. Social interaction plays a viable role in the early infants life, but following developmental psychology, early social interaction does neither require sophisticated perceptual abilities nor elaborated motor skills (Stern, 2002, 2009). In Stern's social interactionist view, early parent-child communication occurs via social contingencies in an overall temporal flow of patterns of intensity differences. Such differences in the intensity of experience could for instance be uttered in sound and answered in touch by relating to the velocity or pitch envelope of the sound in the dynamics of touch, establishing inter-subjective contact. Stern argues that the infant initially does not perceive these signals as visual or kinaesthetic but rather as a transmodal "dynamic of living" in a space spanned without clear distinction between the modalities by external and internal sensations. Stern argues that a transmodal mode of perception allows the infant to make contact with its social world in relation to her needs long before she can properly hear, see or move. Transmodal mother-child communication may be seen as a primary form of sense-making, and once established, it becomes a major emotional-motivational source that supplies movement intentions for goal-directed motor learning and the transition from pre-reflexive to reflexive communication and the experience of life (Stern, 2009). Recently, experiments on perceptual crossing have been established to investigate such a minimal form of sense-making in social interaction dynamics. Perceptual crossing denotes the mutual recognition of human observers in an interactive setting such as making eye contact. Experiments on tactile perceptual crossing via movement dynamics in a shared uni-dimensional tactile space highlight that mutual-recognition in these experiments is not a passive perceptual act of either observer but arises from a circular interaction dynamics that is elicited by the mutual engagement in recognition activity (Auvray, Lenay, & Stewart, 2009; Di Paolo, Rohde, & Iizuka, 2008).

3.4.7 Enactive Attention And Salience

Interestingly, albeit attention is a major topic in mainstream cognitive science, it has not been addressed systematically within enactive work²⁸. One reason may be that the program is in a transition from a theoretical-conceptual level to experimental research (Bechtel, 1988; Di Paolo et al., 2010; Schumann, 2004). The following brief sketch indicates that the enactive framework poses the need for a novel conceptualization of attention in reference to autonomy, adaptivity and sense-making, with the particular to work out an account of spontaneous attention (section 3.3.3).

²⁸ I am thankful to Diego Cosmelli, Evan Thomson, Michel le van Quyen and Jean-Philippe Lachaux for information on enactive accounts of attention.

What is the role of salient features in sense-making in an enactive account of (visual) salience? The basic assumptions for this outline are that enactivism construes perception and action as aspects of sense-making processes; that moving gaze is one fundamental way to engage in sense-making; that visual salience singles out discriminatory features in the visual-spatial sensorimotor space, and that discriminatory features are a useful concept also in enactive analysis. Then enactive theory suggests that visual salience is related to a spatial-visual differentiation of meaning that is created in sense-making within a three-dimensional space. Therefore the function of salience would not be to represent objective properties of the spatial world as in bottom-up manner information processing accounts. If visual features result from discriminations in sense-making processes, they rather reflect meaningful discriminations in relation to the full spectrum of meaning contexts involved. From the mind-life continuity hypothesis, relevant contexts include motivational, emotional or social levels of analysis. Enactive work on the concept of salience will thus, as Marek McGann points out (in personal communication, 2012), require a theory of context. To the degree to which sense-making is a skilful activity, enactive work on salience will also address the embedding of salience in the learning of skills as well. Skilled training within a context leads to novel abilities for discrimination, which become salient and attract attention once established within the respective context. An enactive theory will also address the difference between salience in the point of view of the observer (i.e. the scientist) and salience in the point of view of the perceiver (i.e. the subject), as the concept of enactive autonomy wishes to naturalize genuine meaning in the perspective of the observer. Hence if salient processes occur as an aspect of sense-making, salience is specific to the individual perspective and meaning contexts of the observer. In this respect, one particularly interesting question is whether third person principles can serve as third-person constraints for first-person visual sense-making behaviour, and if this link shows potential to link classical and enactive approaches to salience and attention.

4 Summary and Discussion of Papers Represented in This Thesis

We use an innovative eye-tracking system (EyeSeeCam, Schneider et al., 2009) to record the visual input of human observers in gaze-contingent and head-contingent video recordings. Gaze is measured as a function of whole body movements in the world during spontaneously occurring motor behaviour. Observers explore and navigate through real-world environments in the absence of a specific experimentally given task. The obtained visual stimulation approximates the observer's perspective and thus is at the same time a result of past and an origin of future spontaneous behaviour. We analyse spatial and temporal aspects of human gaze movements in natural situations and compare natural human eye movements to the laboratory as well as to similarly recorded natural eye movements of the cat.

4.1 Salient Features at Gaze

In our main result, we find that local salient image structures accumulate at the centre of the gaze-centred video recording. Hence during natural exploration behaviour, human observers actively direct gaze to structural aspects of the world. This demonstrates that the concept of feature salience transfers from laboratory settings to real world scenarios (**Study 1**).

To directly compare eye movements in free exploration and laboratory, we replayed the head-centred video recordings in a standard eye-tracking setup. Eye positions obtained under continuous replay predict the corresponding real world gaze better than eye positions on static images (of 1s duration). This deviation may be explained by the time a bottom-up signal needs to be processed and to trigger an eye movement with the frequent onset of a novel stimulus in the display of static images. In addition, a bottom-up salience model predicts observers' eye positions better with dynamic stimuli, demonstrating that preserving natural temporal stimulus properties improves the ecological validity of experiments and models (**Study 3**).

4.2 Spatial Biases

The analysis of spatial feature distributions reveals that in head-based coordinates, local features in the real-world data exhibit off-centre spatial biases that depend on the specific environment, which eye-in-head movements centre in gaze-coordinates. Therefore central feature biases in "natural" photographs are likely a result of already-gaze centred images by the photographer (photographer bias). A centring of off-centre biases in head-coordinates by the eyes also indicates that the central biases in subjects fixation distributions do not result from a pure re-centring of the eyes in orbit, as suggested previously (Tatler, 2007). The analysis of the camera-control signals however does show a weak central bias of gaze-direction also during natural exploration (**Study 1 and Study 3**). With naturalistic interaction of body, head and eyes within the demands of the world, these may however not result from a re-centring of the eyes in their head-based orbit per se, but from a frequent co-alignment of gaze- and head direction in whole-body actions.

In the laboratory replay, the static 1s replay condition shows the highest inter-observer consistency of eye positions, but also the strongest central bias of fixations, such that the inter-

observer consistency can mostly be explained by spatial biases that are independent of the stimuli shown. Further, the time course of this central bias suggests that the (unnatural) stimulus onset of a novel picture triggers a reset of the eyes to centre, potentially for an optimal starting location for early scene processing when the screen is limited (Tatler, 2007).

In sharp contrast, the distribution of gaze in free exploration suggests a spatial bias towards the path walked on. This task-dependent bias is found to be weaker and of less contextual relevance in the laboratory condition. Thus naturally occurring behavioural tasks may form specific implicit priors for the distribution of the eyes, consistent with a function of gaze movements in picking up task-relevant information at anticipated points-of action (Hayhoe & Ballard, 2005) (**Study 3**).

These results implicate that research on visual attention that focuses on eye-in-head movements *should* use biased stimuli with realistic biases obtained in natural recordings in human head-centred coordinates. Further, spatial biases from tasks and motor planning should be incorporated in future sensorimotor models of visual attention.

4.3 Distinct Roles for Eyes- and Head in Allocating Gaze

Global power spectra revealed distinct classes of scene layouts in the environments recorded. Closed and indoor environments show anisotropic signatures with emphasized horizontal and vertical spatial frequencies and spatial constraining by large buildings and walls. In contrast, open environments show more equally distributed power spectra along frequencies of all orientations. These results confirm image-based scene-categorization (Torralba & Oliva, 2003) in natural human visual input. However, we could not observe differences in global power spectra between head- and eye coordinate systems, suggesting that scene layout of natural visual input operates on a large spatial scale compared to eye-in-head-movements and is a consequence of head-in-world rather than eye-in-head movements (**Study 1**).

We find a higher-level feature, defined in true and false positive responses of a face detection algorithm, to accumulate near the centre of both head and gaze recordings, but with different function of eye and head. From the comparison of environments with few or numerous true faces, we infer that spurious responses of the higher-level face feature are centred primarily in a coarse allocation of gaze via head-in-world movements up to only several degrees of retinal eccentricity. Eye-in-head movements then accomplished finer gaze-allocation for true faces. We speculate that eye-in-head movements only refine gaze after additional stages of processing, such that candidates of faces are determined in periphery and centred by head-movements but finer gaze-allocation by eye-in-head movements only occurs if candidates are confirmed as true faces. From the present data we cannot confirm that spurious face detection or a correlation with lower-level features is the causal factor attracting attention and gaze. Notwithstanding, our results indicate distinct roles for eye- and head movements and thus highlight the importance of extending computational models to a definition of gaze adjustment that includes the movements of body, head in addition to the movements of the eyes (**Study 3**).

4.4 Temporal Dynamics of Eye-Head Integration

As expected, the analysis of the temporal movements characteristics in both cameras demonstrated that the largest fraction of co-occurring eye- and head movements shows opposing, compensatory movement directions that can serve to stabilize gaze. Yet, movement of gaze is only slightly more stable than movement of the eye and head alone. Surprisingly, a substantial fraction (about 20%) of reflexive (non-saccadic) eye movements act synergistically in the same direction to adjust gaze. Hence during natural exploration behaviour, input to the human retina cannot be adequately modelled using fixations and saccades alone. Instead the dynamics of eye and head movements in gaze allocation has explicitly to be taken into account in models based on natural visual stimuli (**Study 4**).

As the cat visual system is frequently taken as a proxy of human vision, we repeated our temporal analysis of eye movements with earlier data of the cat to directly compare eye-head integration between both species. As in humans, the relative contribution of eye-in-head and head-in-world movements in cats was measured during free natural exploration of a natural environment using a lightweight custom-made head-mounted video setup (CatCam). Basic eye-movement characteristics such as velocity were remarkably similar in both species, despite substantial differences for instance in ecological niche, photoreceptor density, and saccade frequency. Coordinated eye and head movements dominate the dynamics of the retinal input also in the cat, yet head movements of the cat operate on a substantially different timescale, showing an approximately 5-fold faster dynamics. The distribution of eye velocities, similar as in humans, shows a bias towards movements that oppose the direction of the head. However, cat eye-movements that oppose the direction of the head are of short duration and low velocities. Considering the asymmetry in these data, many of the potentially compensatory movements in cats cannot be expected to stabilize the image on the retina within short timescales. Hence our data also argue against a primarily gaze-stabilizing role of eye movements in cats during free exploration behaviour (**Study 5**).

In summary, we find that human eye-head coordination entails a substantial fraction of synergetic non-stabilizing movements. Compensatory eye-movements that stabilize gaze do play an even less dominant role in cats. In consequence models and laboratory experiments need to account for the respective input dynamics to obtain validity for ecologically realistic settings for both species.

4.5 Outlook

It is important to point out that while the present findings indicate a role of salient features in sensory processing in natural behaviour, they do not validate a causal role of bottom up salience mapping in attention and eye movement control. In contrast, bottom up models of visual attention may borrow too much from the conceptualization of attention as a pre-processing stage of object recognition in computer vision and the classical salience model may in fact need to be replaced, for instance by the by unsupervised learning of predictive features or by reinforcement learning of task-features in the sensorimotor space (Tatler et al., 2011). This thesis suggests a role of salience and salient features in a sensorimotor account of visual attention. Discriminative sensory features are a fundamental way to relate both brain and perceptual processes to the world. However, they

should be approached as sensorimotor features that discriminate aspects of the world in intentional behaviour. From a signal-processing view, salience in a sensorimotor space might then be a result of prior hypothesis about both the world and about the possible unfolding of actions in a context of the situation, task intentions and the available action repertoire. From an enactive view, salient features may emerge as a result of skilled sense-making processes of the organism as a whole. Future sensorimotor models of salience should thus be approached at the systems level and include motivational as well as affective and individual motor processes and task-hypothesis for eye, head, and body movements in both their temporal and spatial characteristics.

The data of human retinal input during real-world exploration reported in the first study (Schumann et al., 2008) has been frequently requested for further analysis by institutions around the world, including McGill University; Redwood Centre for Theoretical Neuroscience, UC Berkeley; DeWeese Lab, UC Berkeley; University of Sydney; Massachusetts Institute of Technology (MIT), New York University (NYU); MPI for Biological Cybernetics, Tübingen and the University of California San Diego (UCSD).

Topics include tests scenarios for predictive attention models on real-world data; the analysis of differences in the feature statistics at different regions of the retina; the analysis of receptive field properties in relation to properties of natural stimuli in fMRI; receptive field categorizations of IT neurons; and the comparison of natural visual statistics during object exploration with the statistics during social interaction with other humans. Further, the presented paradigm allows to quantify the visual input statistics of pathologies such as Parkinson, hemineglect or deficiencies in colour vision (see section 6.1.1), and to investigate the effect of different tasks on visual input within the same real-world environment.

5 Appendix A: Publications

5.1 Study 1:

Salient Features in Gaze-Aligned Recordings of Human Visual Input During Free Explorations of Natural Environments.

Frank Schumann¹, Wolfgang Einhäuser², Johannes Vockeroth³,
Klaus Bartl³, Erich Schneider³, Peter König¹ (2008)

(1) Institute of Cognitive Science, University of Osnabrück, Germany

(2) Department of Neurophysics, Philipps-University Marburg, Germany

(3) Neurology, Hospital of the Ludwig-Maximilians University Munich, Germany

Journal of Vision, 8(14):12, p. 1-17

<http://www.journalofvision.org/content/8/14/12.long>

5.2 Study 2:

Distinct Roles for Eye and Head Movements in Selecting Salient Image Parts During Natural Exploration.

Wolfgang Einhäuser¹, Frank Schumann², Johannes Vockeroth, Klaus Bartl, Moran Cerf, Jonathan Harel, Erich Schneider, Peter König (2009)

(1) Department of Neurophysics, Philipps-University, Marburg, Germany

(2) Institute of Cognitive Science, University of Osnabrück, Osnabrück, Germany

(3) Clinical Neurosciences, University of Munich Hospital, Munich, Germany

(4) Computation and Neural Systems, California Institute of Technology,
Pasadena, California, USA

(5) Division of Electrical Engineering, California Institute of Technology,
Pasadena, California, USA

Annals of the New York Academy of Sciences, 1164, p. 188-19

<http://www.ncbi.nlm.nih.gov/pubmed/19645898>

5.3 Study 3:

Gaze allocation in natural stimuli: comparing free exploration to head-fixed viewing conditions.

Bernard Marius 't Hart¹, Johannes Vockeroth², Frank Schumann³,
Klaus Bartl², Erich Schneider², Peter König³, & Wolfgang Einhäuser¹ (2009)

(1) Department of Neurophysics, Philipps-University Marburg, Germany

(2) Chair for Clinical Neurosciences, University of Munich Hospital, Germany

(3) Institute of Cognitive Science, University of Osnabrück, Germany

Visual Cognition, 17(6), p. 1132-1158

<http://www.tandfonline.com/doi/abs/10.1080/13506280902812304>

5.4 Study 4:

Human Eye-Head Co-Ordination in Natural Exploration.

Wolfgang Einhäuser^{1,2}, Frank Schumann³, Stanislavs Bardins⁴,
Klaus Bartl⁴, Guido Böning⁴, Erich Schneider⁴, Peter König³ (2007)

(1) Institute of Computational Science, ETH Zürich, Switzerland

(2) Division of Biology, California Institute of Technology, Pasadena, CA, USA

(3) Institute of Cognitive Science, University of Osnabrück, Germany

(4) Neurology, Hospital of the Ludwig-Maximilians University Munich, Germany

Network: Computation in Neural Systems, 18(3), p. 267-297

<http://www.ncbi.nlm.nih.gov/pubmed/17926195>

5.5 Study 5:

Eye-Head Coordination During Free Exploration in Human and Cat.

Einhäuser W., Moeller G.U., Schumann F., Conradt J.,
Vockeroth J., Bartl K., Schneider E., König P. (2009)

Annals of the New York Academy of Sciences, 1164, p. 353-366

<http://www.ncbi.nlm.nih.gov/pubmed/19645927>

6 Appendix B: Other Projects

6.1 Visual Attention

6.1.1 EyeSeeCam “Colour-Blind”²⁹

Colour perception in primate vision is often explained by an evolutionary advantage of detecting ripe fruit within the red-green colour axis. We used the methodology and analysis developed in Schumann et al. (2008) to demonstrate the benefit of the red-green colour axis in fruit search in a natural setting. In a pre-experiment, we investigated search in a field of ripe strawberries. Compared to matched healthy control subjects, red-green “colour-blind” subjects indicated a broader distribution of red-green colour features at the centre of gaze. This indicated that colour-blinds made less dominant and less precise use of red-green contrasts when searching for strawberries.

Strawberry fields, however, are structurally dominated by the alignment of strawberry plants in parallel rows across the field. The presence of these prominent colour-independent spatial cues may dominate the search procedure and thus does not allow to single out feature- over spatial effects of “colour-blindness” in visual search.

Hence the main experiment conducted visual search in the presence of a spatially heterogeneous distribution of colours in the experimental field to enhance the discriminatory power of colour features in the search. The revised experiment distributed colourful “Smarties” as targets and “M&Ms” as distractors evenly on a lawn. Preliminary analysis revealed that colour-blinds could use yellow distractors for positive but not for negative pre-selection, suggesting that colour-blinds are impaired in the use of avoidance strategies in colour-based search.

Publications (Posters):

Kugler, G., ‘t Hart B.M., Kohlbecher, S., Bartl, K.; Schumann, F., König, P., Einhäuser, W., Brandt, T., Schneider, E. (2011): Deuteranomaly in natural visual search. Society for Neuroscience Meeting (SfN), Washington, USA, 12.-16.11.2011

‘t Hart, B.M., Kugler, G., Bartl, K., Kohlbecher, S., Schumann, F., Brandt, T., König, P., Einhäuser, W., Schneider, E. (2011): Real-world search strategies with normal and deficient color-vision, 34th European Conference on Visual Perception, Toulouse, France, 28.8. 1.09.2011

Kugler, G., ‘t Hart, B.M., Kohlbecher, S., Bartl, K., Schumann, F., Einhäuser, W., Brandt, T., Schneider, E. (2011): Eye Movements in the real world during visual search for colored candies, Basic and clinical oculomotor research – A tribute to John Leigh, Puerto Madera, Argentina, 25–27.3.2011.

²⁹ Contribution: experimental design, conducted, analysed and interpreted pre-experiment, provided data analysis methods.

Kugler, G., 't Hart, B.M., Bartl, K., Kohlbecher, S., Schumann, F., Einhäuser, F., Brandt, T., Schneider, E. (2011) Looking for Candy: Real World, feature based search, 9th Meeting of the German Neuroscience Society, Göttingen, 23-27.03.2011.

Kugler, G., 't Hart, B.M., Kohlbecher, S., Schumann, F., Einhäuser, W., Brandt, T., Schneider, E. (2011): Farb- und formbasierte visuelle Suche bei unterschiedlichen Farbsehfähigkeiten in natürlicher Umgebung, 55. Jahrestagung der DGKN, Münster, 16-19.3.2011.

6.1.2 Empirical Saliency Matlab Toolbox

My master thesis presented a data-driven Bayesian model for the influence of individual visual and their integration on visual attention. The methods proved viable as a standard analysis across a major number of eye-tracking studies conducted within the laboratory. To ensure comparability between these projects and to reduce errors and implementation time, we developed a Matlab toolbox for Bayesian estimation of empirical feature-saliency functions including a detailed documentation.

6.1.3 Empirical Saliency Baseline Study

We also conducted a baseline study to obtain saliency models for a substantial number of visual features in the absence of experimental tasks or stimulus modulations on a large set of natural images. The latter aspect has been performed in the Bachelor's thesis of Anke Walter, supervised by Peter König and Selim Onat, and unofficially by myself. The Empirical Saliency Toolbox as well as the image set and baseline data have been used in many experiments in the Neurobiopsychology Lab since.

6.2 Sensory Enhancement (feelSpace)³⁰

The following provides an overview of my work as project leader within the feelSpace project (see also Figure 1-1: Contribution to the feelSpace project. It is not intended as a comprehensive documentation and should not be taken as such. Further documentation is provided elsewhere internally.

Sensorimotor approaches to perception have gained a substantial part of their experimental support in studies on sensory substitution (Bach-y-Rita & Kercel, 2003). Sensorimotor accounts argue that a modality such as vision is not specified by a specific cortical area that gives e.g. a visual perceptual interpretation to the signals of the eye, but by specific sensorimotor contingencies that create a specific mode of visual sensorimotor organization. Consistent with this, sensory substitution experiments could show that some aspects of visual perception can be achieved via a presentation of visual signals over another sense organ like the skin (Bach-y-Rita, 2004) or the ears (Auvray, Hanne-ton, & O'Regan, 2007). However, a problematic aspect of the argument from sensory substitution is that even in congenital blindness, some innate cortical specialization for vision may still be in place and responsible for the perceptual quality achieved through the substitution. A previous pilot study investigated sensory enhancement as a novel experimental paradigm to overcome this limitation. Adult subjects receive novel orientation information unavailable through the natural senses, obtained by a magnetic compass, via vibrotactile stimulation around the waist (Nagel et al., 2005). The results provide conceptual prove that it is possible to influence physiological reflexes and the quality of perception by an introduction of novel perceptual sensorimotor contingencies.

The follow up projects presented here study the neural substrate of newly acquired perceptual sensorimotor contingencies with physiological techniques; introduce quantitative measures of cross-modal integration into the sensory enhancement paradigm; test the usefulness of the directional information for congenitally blind individuals; and characterize changes in the perceptual quality induced by the novel sensory information using novel methods for the acquisition of data about subjective experience. In summary, these projects present the unique opportunity to relate the neural substrate of novel spatial sensorimotor contingencies and their influence on behavioural performance and perception.

Publiations (Posters):

König, S.U., Brunsch, V., Ebert, M., Fleck, S., Gameiro, R., Gasse, S., Goeke, C., Hanke- Uhe, M., Kaspar, K., Keyser, J., Krause, C., Lytochkin, A., Muil, R., Numonov, A., Sieveritz, B., Schmitz, M., Wache, S., Nagel, S.K., Schumann, F., Meilinger, T., Bülthoff, H., Wolbers, T.,

³⁰ This section is based on my final draft for the grant proposal „Sensory enhancement – learning a new sense“ to Deutsche Forschungsgemeinschaft (DFG) and the abstract „Sensory-enhancement with a haptic compass (feelSpace) in a congenitally blind subject“ by Anna-Antonia Pape, Frank Schumann, Anna Best, Brigitte Röder, Peter König (submitted to ASSC).

Büchel, C., König, P. (accepted): Properties and mechanisms of sensory enhancement, Spatial Cognition 2012, Kloster Seeon, 31.08.-03.09.2012

Ebert, M., Fleck, S., Goeke, C., Kaspar, K., Keyser, J., König, S., Krause, C.D., Muil, Nagel, S.K. Schumann, F., König, P. (2011). FeelSpace: A holistic study of sensorimotor contingencies. Banff Annual Seminar in Cognitive Science.

6.2.1 Hypothesis

Providing information on the environment not covered by an existing sensory organ raises many questions, which we formalize in six hypotheses:

1. Weak Integration

The information provided by the belt with respect to magnetic north is processed and leads to an improvement in performance in some situations that are adequately described in an allocentric coordinate system.

2. Strong Integration

The information on orientation with respect to magnetic north is firmly integrated into sensory information provided by all the senses. Sensory signals of the belt inconsistent with sensory inputs provided by the other modalities produce measurable responses.

3. Automatic Processing

The information provided by the belt with respect to magnetic north can be processed at least in part without the need for attention, and is of behavioural consequences expressed in alterations of reflexes.

4. New Modality

The information provided by the belt leads in interaction with overt behaviour to qualitatively new sensory experiences beyond the tactile stimulation proper.

5.a Low-level modality specific processing

The physiological and psychological effects are mediated by alterations in primary sensory areas. As a corollary, the effects are limited to part of the somatosensory topographic maps, as predicted in the enactivist account of O'Reagan and Noë (2001).

5.b High-level modality invariant processing

The physiological and psychological effects are mediated by alterations in multimodal areas beyond primary sensory areas. As a corollary, the effects extend beyond the sensory sheet involved in training and encompass a larger part of the topographic maps, as predicted by hierarchical accounts of sensorimotor contingency learning.

6. Correlation

Individual differences in cortical integration of the information about north lead to individual differences in the psychological utilization of the information about north.

The following provides a short overview of the experiments that were developed for this ambitious project.

6.2.2 Belt Development

We developed a novel piezo-electric variant of the belt that is electromagnetically compatible with magnetic resonance imaging environments. As we are particularly interested in the physiological correlates of mastery of the directional information within the belt stimulation, a concomitant mobile version of the belt uses identical piezo-electric actuators. This ensures that the purely tactile aspect of the vibro-tactile stimulation is identical in daily training and fMRI experiments. Hence found effects are not dominated by surprise or adaption to a novel, different type of vibro-tactile stimulation that subjects encounter only during fMRI measurements.

Belt development followed an iterative process in particular with respect to electromagnetic artefact reduction in the MRI environment and with respect to providing mechanically stable housings to the fragile piezo-ceramic actuators chosen. A detailed description of the development process is given in a bachelors thesis (Keyser, 2010) and the report of the study project feelSpace II (Ebert & Muil, 2010), both supervised by Peter König and myself.

6.2.2.1 Magnetic Resonance Imaging (MRI) Compatible Piezo Belt

6.2.2.1.1 Tactile Actuators

MRI actuation methods are an important field of medical robotic applications in the MRI environment. For MRI compatibility (Gassert et al., 2006; Tse et al., 2009), we replaced conventional electrical pager motors by MRI compatible piezo-electric bending actuators (PL 140.10 Bending Actuators, PI Physikinstrumente GmbH, Karlsruhe). Among the MR compatible actuation devices (Gassert et al., 2006), piezo-electric vibration elements have been used in fMRI studies of the somatosensory system with need of repeatable and controllable vibro-tactile stimulation with respect to stimulus frequency and intensity (Francis et al., 2000; Harrington & Hunter Downs, 2001; Harrington, Wright, & Downs, 2000). Due to their comparatively low driving voltage of 0-60V, PL140.10 piezo actuators are recommended for medical usage while still providing a high nominal displacement of 1000 μm . Additionally, a fast activation onset below 10ms ensures almost instantaneous update of the tactile signal free of noticeable latencies.

6.2.2.1.2 Piezo-Housings

We developed customary housings to provide a stable case for the mechanically fragile piezo-ceramic elements and for physical mounting of actuators in the belt. Housings contain soldering points, provide additional electronic insulation and enhanced stress relief to handle the special MRI cabling (Figure 6-1).

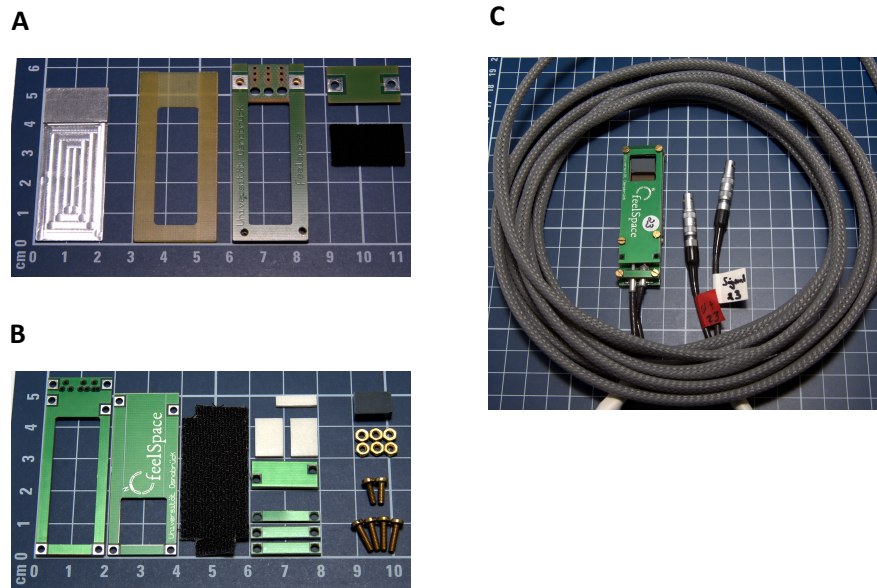


Figure 6-1: Piezo Actuator Housings.

Custom made housings to provide electrical mounting with mechanical stability to fragile PL 140.11 piezo bending actuators. (A) Early variants of the piezo housings based on aluminium and PCB material. (B) Mounting kit of final piezo housing based on robust PCB material. (C) Piezo actuator with shielded coax-cable and high-quality LEMO connectors for use in the MRI environment.

6.2.2.1.3 MRI-Compatible Cabling

To minimize electromagnetic interference, in the MRI-environment piezo actuators are cabled with two coaxial cables of 5 meters length and the MRI control electronics and power supply are placed at a maximum distance from the scanner coil. The wiring keeps the two power signal lines of the piezo (+ and -) separate to further minimize electromagnetic interference (Figure 6-1 C).

6.2.2.1.4 MRI-Belt-Electronics & Electromagnetic Shielding

The core electronics of the MRI-belt is electrically isolated from the experimental control setup outside the scanner via an optical cable. The housing provides efficient shielding against electromagnetic disturbances of both the belt-control electronics as well as the fMRI equipment. Hardware shielding is achieved via multiple solid aluminium boxes for each core component that are placed within a closed aluminium box. The core electronics contains the piezo power supply via lead acid batteries, an optical receiver to decode the optical outside control signal, a microprocessor, optical relays to generate the piezo-driving signal, an optical relay board to switch on the respective piezo actuator (Figure 6-2 and Figure 6-3). Electrical shielding against electromagnetic disturbance is achieved via 60 dB low-pass filters at 120 MHz (approximately the

magnetic resonance frequency of protons at 3 Tesla (T)) on each piezo channel. Filters are build of 3 terminal capacitor T-filters and lead-through chassis PI- filters that connect the signal ground to the shielding aluminium case. A further BCN connector in turn yields low-impedance grounding of the aluminium case on the Faraday cage of the scanning room, such that high-frequency noise can be effectively grounded. Piezo cables are connected via high-functional LEMO connectors.

6.2.2.1.5 Optical-Control-Electronics

Custom made electronics takes control signals via a serial-interface from the experiment computer and delivers a pulse-width modulated optical control signal to the MRI-belt-electronics (Figure 6-2 B) .

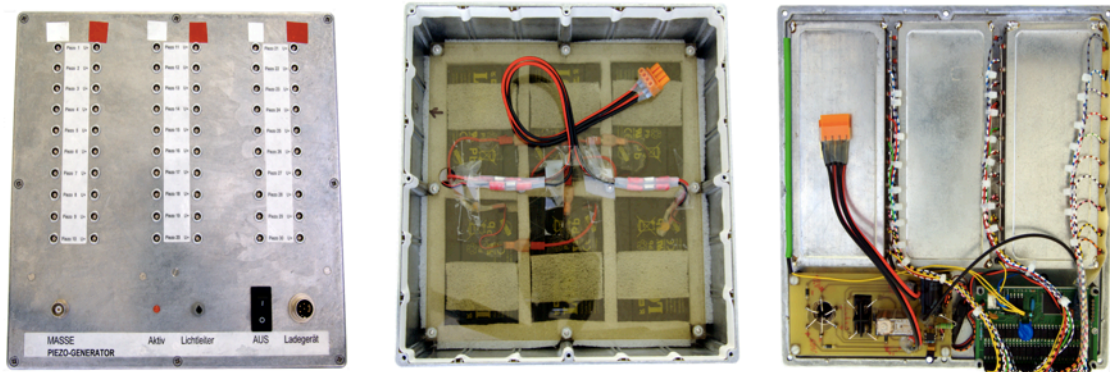
6.2.2.1.6 MRI-Compatibility Testing

In iterative electronics development cycles, we excluded further sources of artefacts in each iteration by tests at the UKE MRI scanning facility in Hamburg. The final development operates without noticeable disturbing cross-influences between scanner and belt equipment (Figure 6-4).

6.2.2.1.7 MRI-Safety

The belt proper has been designed considering MR-safety requirements (Schenck, 2000). While for outdoor application the belt is operated via the attached control unit and compass, in the MR setting the belt proper is placed in the scanning room on its own and interfaced from outside via optical signalling. Potential heating of piezo-ceramics induced by electromagnetic interferences has been tested with an infrared camera system and yielded no increase in the piezo temperature above body temperature during operation (Figure 6-4 E).

A



B

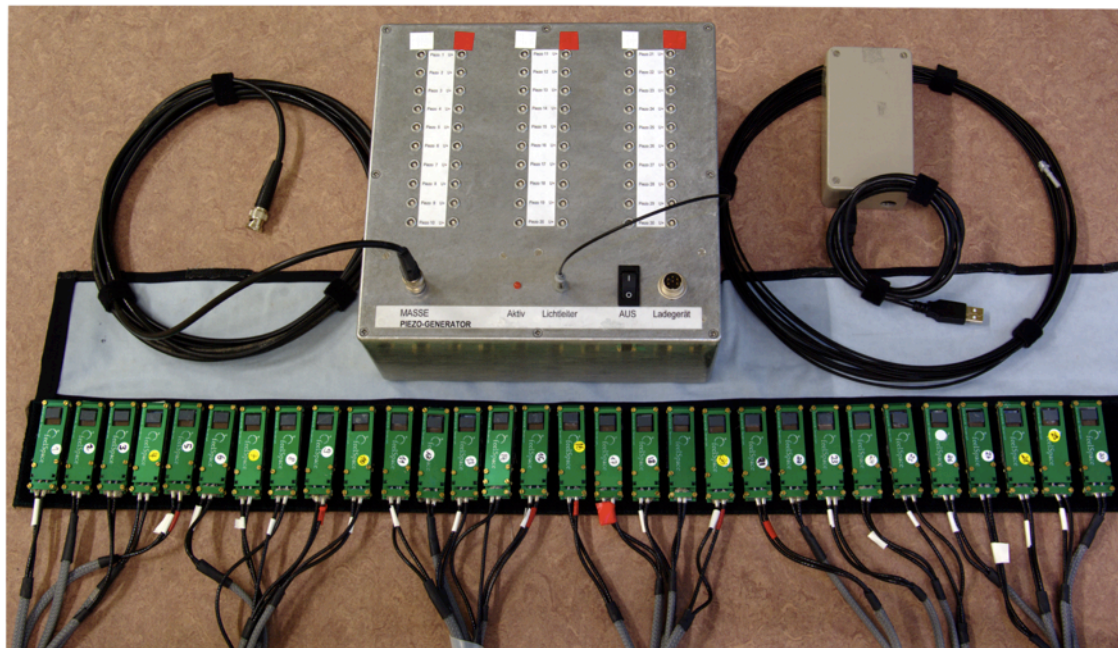


Figure 6-2: fMRI-Electronics and fMRI Belt.

(A) Aluminium shielded control electronics containing lead acid batteries, microprocessor, optical signal receiver and 60 dB electromagnetic filters. Control electronics is placed inside scanner room. (B) The complete fMRI belt setup with outside scanning room optical signal generator, optical cable, inside scanning room control electronics, BNC cable for grounding on the scanners Faraday cage.

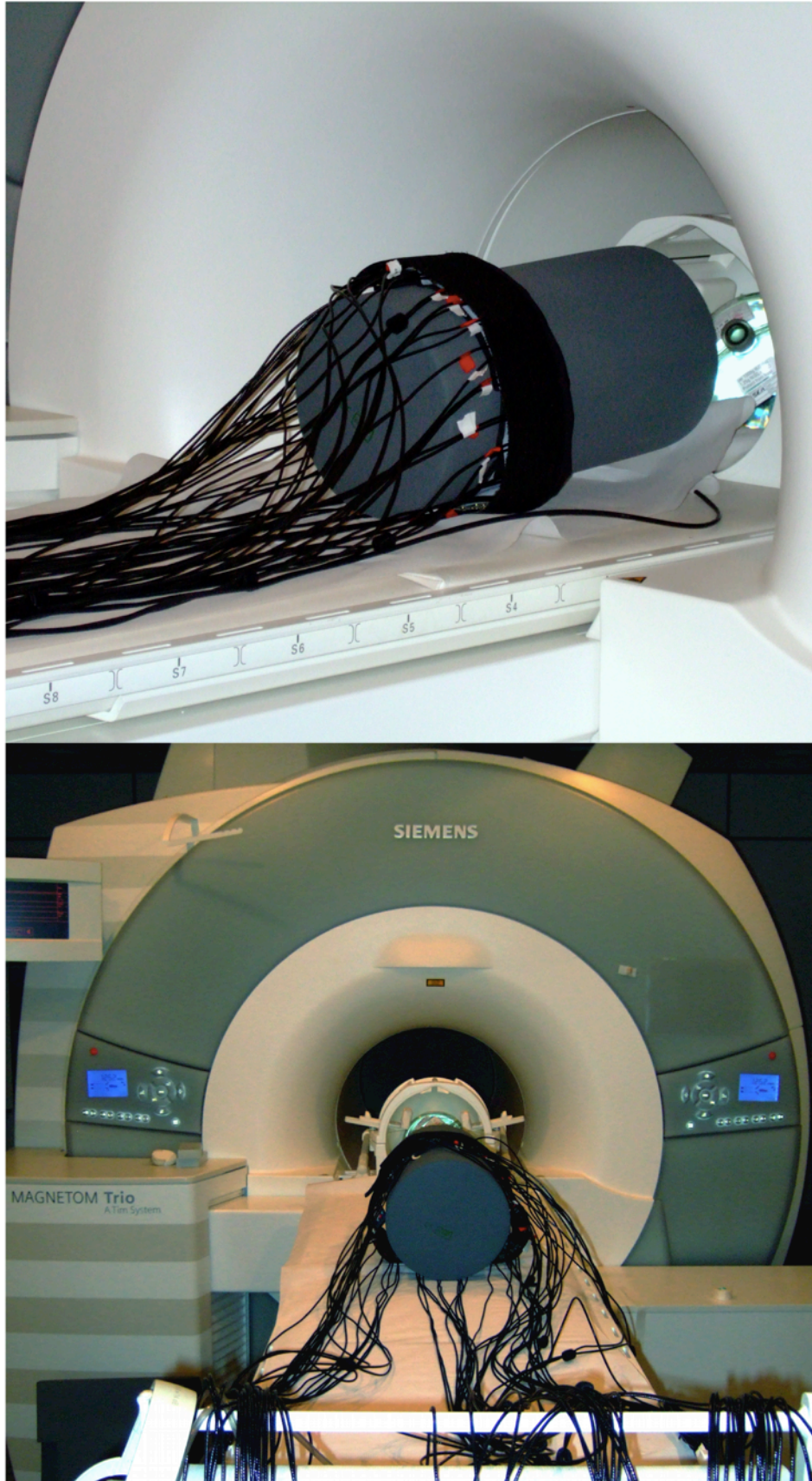


Figure 6-3: fMRI feelSpace Belt Setup for Electromagnetic Testing

fMRI feelSpace belt placed in the scanner prior to electromagnetic testing using an artificial glass head and a BNC cable simulation of the human body.

6.2.2.2 Mobile Piezo Belt

A concomitant mobile variant of the piezo belt ensures an identical nature of the tactile aspect of the vibro-tactile stimulation during both learning and experiment. The mobile belt electronics has been developed with respect to size, mobility, electrical protection, data logging and battery lifetime. The required electronics is split into a to casing, a piezo driver and a control electronics case (Figure 6-5).

6.2.2.2.1 Control-Electronics

The electronics has been prototyped based on the based on the ARDUINO rapid-prototyping platform³¹. It uses an Atmel ATmega328p microprocessor running at 16Mhz at 5V. In the final version, the circuitry has been miniaturized in a custom board layout and custom made casings. The control electronics takes input from the compass, delivers output to the piezo relay electronics, contains power management as well transformation from the battery voltage to the piezo-driving voltage, a GPS sensor, as well as a real-time clock and microSD-card for data logging.

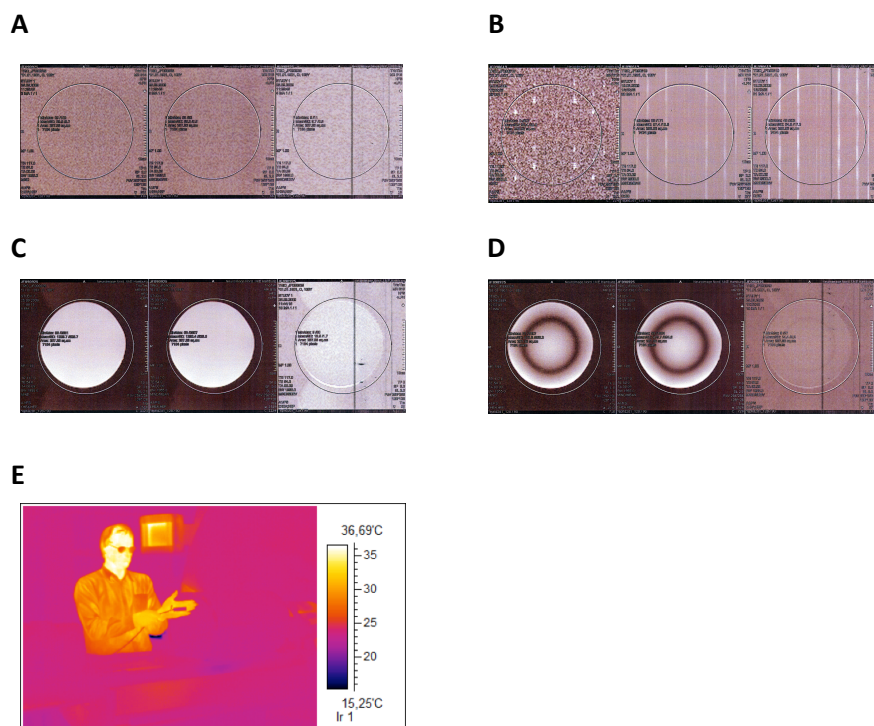


Figure 6-4: Tests of Electromagnetic Artefacts or Heating of fMRI feelSpace Belt.

(A) Baseline sequence without radio pulses. (B) Electromechanical artefacts induced by the first prototype MRI belt. (C) No visible artefacts in the final belt with a spin-echo sequence. (D) No visible artefacts in the final belt with a spin-echo sequence and increased pulse energy. (E) Baseline temperature measurement via an infrared camera. General scanner room temperature is $\sim 23^{\circ}\text{C}$. In the simulation of a broken piezo or cable, a worst-case scenario potentially leading to heating effects, piezo element remains colder than a human hand.

³¹ <http://www.arduino.cc/>

6.2.2.2.2 Compass

Microstrain's 3DM-GX3-25 compass serves as the directional sensing unit. It stabilizes the orientation estimate with addition three-axis gyro and accelerometer data integrated via on-board Kalman filtering. According to Microstrain, the GX3 series provides the smallest orientation sensor of its kind and also lower power consumption than the previous model.

6.2.2.2.3 Piezo-Driving-Electronics

As in the fMRI variant of the belt, piezo actuators are driven by a separate relay circuitry via a pulse-with modulated control signal. On the one hand, this design consideration stems from the separation of piezo-driving electronics via optical cable in the scanning environment. On the other hand, it provides an easy way to distributed the electronics in size and weight around the belt. The vibro-tactile stimulation is nominally provided by a 30 Hz rectangular signal generated by two optical relays that alternatively distribute the piezo voltage and yield high electrical insulation. The signal frequency has been optimized for low power uptake as well as tactile sensibility via prior testing. Current limiters and appropriate resistances secure safe usage of the device.

6.2.2.2.4 Power Supply & Management

The power supply uses three non-magnetic lithium-polymer battery backs with a nominal voltage of 7,4 V and a charge of 2200 mAh each. These are transformed via highly insulated DC/AC adapters to the piezo driving voltage of 22V for electrical insulation and voltage stability. The intensity of piezo actuation is stable over the entire battery lifetime. A power management circuit detects low-voltage state of the battery and triggers an ordered shot down of the electronics when the battery voltage drops below 18V. Shot-down ensure enough battery lifetime to safely close the logging data files on the microSD card as well as a deep de-charging that is damaging to lithium polymer-polymer batteries.

Conventional batteries act as magnets. To not disturb the magnetic sensitivity of the compass with respect to the magnetic field of the earth, various battery options and magnetic shielding have been tested and eliminated before choosing the non-magnetic lithium-polymer batteries used. Additional safety-precautions had to be taken for a safe usage of the lithium-polymer packs in case of accidents. The theoretical current uptake of the piezo actuators given the piezo capacitances, voltage and frequency is 14.4 mA, in practical measurements around 20 mA. This allows a full wake day of belt operation without recharging.

6.2.2.2.5 GPS

GPS data is acquired using the common EM-406A unit from USGlobalSat Incorporated and interfaces directly with the microprocessor via hardware serial TTL connection.

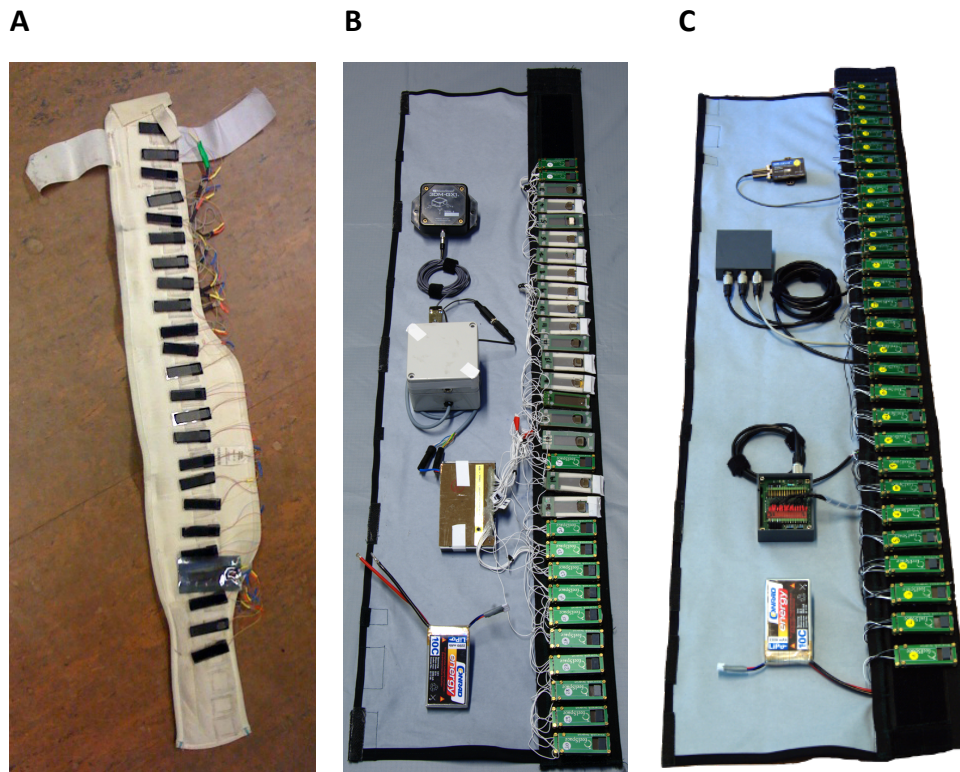


Figure 6-5: Prototypes and Final Version of Mobile Piezo Actuator Belts.

(A) Rapid-prototype as a conceptual proof. (B) Fully functional prototype. (C) Final miniaturized belt design, including compass, piezo-driving electronics, control electronics, 30 piezo actuators in custom made housings, and 1 (of 3) lithium-polymer batteries. Not depicted are LiPo-Safety Bags.

6.2.2.2.6 Mobile-Piezo-Housings

As in the fMRI variant of the belt, robust custom-made housings of the piezo-ceramics were manufactured out of robust PCB material. Further adapted fMRI housings for mobile requirements to provide better stress relief of the cabling and smaller housings.

6.2.2.2.7 Electrical Insulation

Piezo-actuators were electrically insulated using an acrylic thin film coating (Bectron® PL 9915/220-6 VP) at a professional external conformal coating service provider. Both the total voltage isolation of the lacquer and the long-term applicability were tested also via external testing services in electrical breakdown tests (UN Gerätebau, Osnabrück) and long-term mist chamber tests (ELANTAS Beck Electrical Insulation, Hamburg), respectively. All exposed electrical contact points such as soldering points were isolated using the lacquer.

6.2.2.2.8 Fire Protection

Under certain seldom circumstances broken piezo elements can produce sparks that potentially may ignite fire. This risk was taken serious by testing all materials in close contact with the piezo for flammability. The PCB material of the piezo housing is non-flammable by design, only the Velcro used to mount piezo housings into the belt were flammable under contact with bare flames. To further reduce the risk of propagating sparks by braking a potential spreading chain of the sparks, a flame-retardant industry paper (Nomex[®]) is placed between Velcro and the piezo ceramic.

6.2.2.2.9 Water Protection

The entire piezo belt is protected against splash water using a flexible water resistant Lycra textile (LY242DX, Toray International) in a custom made design.

6.2.2.3 Mobile Pager Belt

A design goal of the entire development process has been the subsequent development of a next generation pager motor belts with minimal changes to the central hardware, software and data logging abilities. Partly motivated by this future aspect, much work has been invested into the miniaturization of the control electronics and the division between general (e.g. compass, GPS, logging, power management) and piezo-specific (e.g. relay board, fall out detection) hardware.

6.2.2.4 Setup of Electronic Workshop and Internal / External Collaborations

For a conceptual proof I extended the original feelSpace belt with piezo-electric actuators in rapid prototyping by myself. Further iterations of the belt have been developed in close cooperation with the electronics- and mechanics workshop of the University of Osnabrück and within a study project of Robert Muil as well as the bachelor thesis of Johannes Keyser. I maintained contact with experts in magnetic resonance imaging electronics (Mr.confon, Magdeburg) and electric insulation security (Staabsstelle für Arbeitssicherheit, Universität Osnabrück; BueroVeritas, Zertifizierungsstelle für Medizingeräte, Türkheim; ELANTAS Beck Electrical Insulation, Hamburg; UN Gerätebau, Osnabrück). The mass production of belts was performed by student research assistants and by myself. I was involved as organizer, supervisor and practical worker in all major and the vast majority of minor design decisions during the entire development and also the production cycle.

6.2.3 Training

To give behavioural relevance to the information provided by the belt, a training period of 6 weeks begins immediately after the pre-training tests. Experimental subjects are required to wear the belt during waking hours over the entire training period and exert a substantial amount of outdoor activity each day. They are also encouraged to take daytime sleep periods when they feel the need of sleep to foster cortical learning processes. A part of the required usage time consists of additional outdoor training sessions. Because we expect most noticeable effects in the beginning, the additional training will initially be scheduled tight with two daily training session in the first five days, followed by a two-day resting period free of training, and a second five day period with additional training twice daily. For the rest of the training period, additional training (beyond usage in normal behaviour) will be only once a day to encourage natural usage of the new device. A simple training task is directional pointing, but more complex tasks have been evaluated in addition following Awareness Through Movement principles. These tasks are documented internally elsewhere. In the exemplary pointing task participants have to stand at a starting position in an empty area facing a clearly visible reference point. Afterwards they are blindfolded and have to move around, following the verbal instructions of a supervisor, such as ‘Turn 45° to the left, now walk 10 steps.’ The numbers of instructions in each run varies, leading to different complexities of runs. After each run, subjects will be asked to point to the direction of the reference point they faced in the beginning. Then they are allowed to remove the blindfold to see how they had performed.

More intense daily practice and usage of the belt during training should lead to more intense learning of the belt sensorimotor contingencies. We aim to relate the learning performance to the natural daily usage of the belt and log the compass signals as indicator of daytime movement activity. Further we use a medical activity monitoring system (Cambridge Neurotechnology Ltd, Cambridge) to quantify sleep as well as daytime napping periods.

6.2.4 Physiological Integration: Sleep Electroencephalography (EEG)

There is ample evidence that rich stimulation and learning during wakefulness induces regionally specific and use-dependent sleep processes important in synaptic reorganization (Finelli, Baumann, Borbély, & Achermann, 2000; Vyazovskiy, Borbély, & Tobler, 2000). REM and non-REM sleep phases in particular have been related to procedural and declarative learning, respectively (Plihal & Born, 1997; C. Smith & Lapp, 1991). Furthermore, recent findings in sleep research demonstrate that performance in learning tasks improves with sleep, and that this improvement correlates with changes in local slow-wave and spindle activity in sleep EEG over the circumscribed brain areas that are active in the task itself. Hence, we aim to measure local changes in sleep phases and sleep EEG activity as a physiological correlate of the learning induced by training with the belt (Correlation Hypothesis).

6.2.5 Behavioural Integration: Homing

We use the well-known homing task to test whether the additional information provided by the belt helps to update observers spatial position during path-integration (Loomis et al., 1993; Riecke, Bühlhoff, & Veen, 2002; Stepankova, Pastalkova, Kalova, Kalina, & Bures, 2003). The pilot study (Nagel et al., 2005) could show that training with the direction information provided by the belt can improve performance in homing. This part aims to replicate these previous results using a refined experimental design.

Humans and most animals are able to update their spatial position to be able to return to a starting point relying on multimodal self-motion cues only. This process is referred to as path integration. Path integration combines visual cues or localized sounds as well as internal proprioceptive and vestibular signals into a homing vector that points to the starting point (“home”) and is continuously updated during their entire outbound journey. The homing vector allows to home back on a self-generated path without using learned landmarks or an allocentric survey representation of the path travelled (Etienne & Jeffery, 2004; Etienne et al., 1998; Etienne, Maurer, & Séguinot, 1996; Sun, Campos, & Chan, 2004).

However, humans have been found to prefer a configural strategy based on survey representations in classical homing tasks (Wiener, Berthoz, & Wolbers, 2011), rendering experimental designs for studies of human path integration more complex. Following the classic encoding-error model humans spontaneously decompose the travelled path of simple polygons into their elements and then reconstruct the homing vector based on a survey representation of the figure (Fujita, Klatzky, Loomis, & Golledge, 1993). Ego-centric path integration has been induced in humans by more complex figures and by explicit task instructions. First, increasing the number of segments in the homing figure surprisingly reduces the reaction time of the homing response with path length and total angular turning kept constant. Such shorter response times have been taken as an operationalization for a switch from a configural strategy to path integration processes with more complex figures. During path integration, the homing vector is continuously updated during the entire journey. The pointing response under path integration can rely on the homing direction in short-term memory without additional path reconstruction prior to pointing. Configural strategies by contrast should yield slower but not faster responses when the complexity of the figure and the reconstruction of their elements increase. Hence a switch from slow configural to faster path integration strategies with more complex figure explains the observed reduction of response times. Curved elements reduce the clarity of the figure tremendously and render a configural solution more difficult, similarly to hexagon path layouts (Lafon, Vidal, & Berthoz, 2009) and layouts with crossing paths (Klatzky et al., 1999). Hence natural paths in urban environments with complex layouts and curved lines should induce a path integration strategy in humans as well. Lastly in a recent study could induce dissociable path integration vs. configural strategies by explicit verbal instructions. Instruction observers to continuously integrate the path during the journey yielded faster pointing responses, whereas a configural instruction yielded more precise estimate of the home direction but with slower responses (Wiener, Berthoz, & Wolbers, 2011).

6.2.5.1 Methods

To minimize confounding influences of the remaining modalities, path integration will be performed indoor in large quiet room to exclude external cues from wind direction or sunlight. Furthermore, participants will be blindfolded and hear auditory white noise via headphones.

Triangular figures are frequently used in the homing literature and would allow direct comparison of homing with the belt to previous experiments. However, our primary concern is not in the comparison with the homing literature but in the comparison before and after training with the belt information. Hence to bias our subjects as strongly as possible towards path integration strategies, we will use complex figures with curved lines but without intersections and provide explicit task instructions for path integration. Walkers will be guided to a point in this space (the homing point) and asked to memorize its location. Afterwards, subjects will be lead along shapes of varying complexity. They are explicitly instructed to continuously imagine and update the location of home during the entire figure, and to quickly and accurately point towards the location of the homing point at the end of the figure. The ideal route is the edge connecting the current position directly back towards home. We measure the angular deviation between the indicated and ideal homing vectors and the reaction time of the response. We will use homing shapes of different complexity classes with 15-20 trials each with and without belt each. To avoid feedback about the end position of the previous trial, novel figures will start at a novel homing position different from the the previous figure. Conditions will be balanced with respect to the presence of belt input and order of the figures.

6.2.5.2 Analysis

The homing literature predicts an interaction between angular turning and path length after training. Homing errors accumulate over path length and over the size and number of angular turnings, while the belt signal gives more stable feedback selectively on angular turning but not path length. Further, within a configural strategy, the belt likely is useful for the separation of a figure into components. This predicts an increase in performance (smaller pointing errors) in trials with longer reaction times that are associated with a configural pointing strategy.



Figure 6-6: Indoor Homing Setup in Large Hall.

Homing experiments assess the influence of the directional belt information into behaviour. Experiments will be performed in large-scale, quite and closed hall. Subjects will be blindfolded with blackened swimming goggles and wear earplugs to exclude external directional cues such as wind or temperature gradients, noise and sun light. Hence changes in homing performance can be related to mastery of the belt signals alone.

6.2.6 Optimal Multimodal Integration: Psychophysics³²

We developed a turning paradigm in a large-scale virtual environment to quantify if the integration of the belt signal follows the natural rules of sensory integration. Recent psychophysical experiments show that in the normal modalities, multimodal cues integrate in a statistically optimal scheme into perception (Ernst & Banks, 2002; Ernst & Bühlhoff, 2004). Such quantitative experimentation with multimodal integration requires precise control of the stimulation given by the multiple senses. Thus, we perform the orientation tasks in an immersive virtual reality environment: The Cyberneum was recently established for psychophysical experiments on human navigation and multimodal integration at the Max-Planck-Institute for Biological Cybernetics in Tübingen. The key question here is whether the belt information is integrated with information provided by other senses in a statistically optimal fashion. This constitutes a test of the Strong Integration Hypothesis.

Optimal sensory integration predicts that the contribution of a given sensory signal to a multi-modal estimate such as size or location is determined by a linear sum of unimodal signals weighted by the inverse of their respective variance. Thus, if the belt signal is firmly integrated into the modalities by natural optimal integration rules, on the one hand the belt signal should become more influential in the final multimodal turning judgment when the reliability of the natural senses such as vision is decreased by noise. On the other hand, if noise is added to the directional information provided by the belt, the resulting reduction in reliability should decrease the influence of the belt signal in the multimodal estimation.

6.2.6.1 Methods

Participants must judge the angular size of two successive self-turnings in a 2-AFC task. Subjects turn to the left or right until a cue signals the end of the intended turning interval. The virtual environment provides visual flow via a limited-lifetime dot display on a head-mounted display and directional information by the belt signal as well as natural proprioceptive and vestibular information. We test for optimal integration of visual and belt information by adding angular noise to both signals to reduce their respective cue reliability. For both modalities, noise is generated as a parametric sum of Gaussians that is added to the speed of rotation as measured by the compass signal. Noise gradually decouples the angular feedback by belt or optic flow information from the actual angular displacement performed in a random, unpredictable manner. Three noise levels are defined using the parameters of the Gaussians. We determine a psychometric function and a just noticeable discrimination threshold (JND) for each modality in three reliability levels, which serve as unimodal baselines. We test optimal integration by the comparison between the measured bimodal behavioural data against the optimal prediction based on the unimodal baselines. The Strong Integration Hypothesis predicts that the belt signal will be integrated in a more optimal fashion after the training period.

³² This text is in part based on the study project feelSpace II (Ebert & Muil, 2010), conducted under the supervision of myself and Peter König, where also a more detailed report on the psychophysical investigation can be found.

6.2.6.2 Analysis³³

We use of a maximum-likelihood estimation procedure for the fitting of psychometric functions to handle stimulus execution errors as well as a differential log scaling to reduce variance inhomogeneity induced by our self-turning 2AFC paradigm. In self-executed paradigms standard and comparison stimuli are not exact because they result from subjects' self-movement and contain execution error. With exact stimulus presentation, 2AFC tasks yield repetition samples of binomially distributed data for each of the stimulus intensities tested. Then a standard way of fitting a psychometric function uses a regression procedure and the associated goodness-of-fit. However, execution error in the stimuli presentation prohibits repetition sampling of a given stimulus intensity and yields data with one repetition per executed stimuli instead (distributed around the intended value). Hence, we use maximum-likelihood-estimation instead of regression to compute psychometric functions and the associated likelihood as a measure of fit. For the interpretation of the log-likelihood parameter we bootstrap the random distribution of log-likelihoods under the given model (Wichmann & Hill, 2001a, 2001b). For psychometric fitting data will be represented in the two dimensional space between the difference in comparison and standard stimulus on the x-axis of the plot, and the probability $P(\text{Comparison} > \text{Standard})$ of the comparison stimuli being perceived larger than the standard stimulus on the y-axis. Hence values on the y-axis range between the probabilities of 0 and 1 and the JND depicted by the probability of 0.5. Without bias, JNDs will be 0° in all conditions and the difference in conditions will be reflected in the steepness of the psychophysical curve alone.

Second, variance inhomogeneity of our data affects the model fit. Psychophysical data analysis is based on the imperfect nature of the perception of a stimuli and the resulting variance in the perception of the presented stimulus. Hence, every 2AFC comparison in effect represents a signal-detection situation in which a perceptual decision of the observer about the comparison stimulus is modelled not only by the distance to the standard stimulus, but also by the variance in both stimuli. One way of describing the psychometrical function is by integration of signal-detection probabilities over the space of comparison stimuli under the condition of homogeneous variances of all comparison stimuli (Wickens, 2002). However, given the angular turning estimate is likely to accumulate errors over the temporal integration of turning signals, we expect larger angles to have larger errors both in execution and perception and hence show inhomogeneous variances over the stimulus space. To reduce the resulting distortion in the psychometric function, we can transform potential multiplicative into additive noise processes by fitting the logarithm of the difference between comparison and standard stimulus on the x-axis.

The psychophysical literature commonly uses about 400 trials to estimate the steepness of a psychophysical function. Given the 9 (3x3) visual-haptic noise level combinations and the total length of one trial, 400 trials per estimate are not practically applicable. Given the data shows no bias (i.e. all JNDs are around 0° on the x-axis), we can reduce the number of estimated parameters in the fitting model by fixing the JND to 0, effectively reducing the number of trials required for the fit. Maximum-likelihood-fitting of psychometric functions is described in (Wichmann & Hill, 2001a, 2001b). We will use the implementation provided in the Python `psignifit` toolbox (<http://psignifit.sourceforge.net/>) for our data analysis.

³³ I am thankful to Frank Jäkel for discussions about psychophysical data analysis methods for our turning paradigm and for suggesting the `psignifit` toolbox.



Figure 6-7: VR Setp for Angular Self-Turning Experiment in the Cyberneum.

A head mounted display (HMD) provides optical flow via a minimal limited lifetime dot environment. Tracking uses a VISON system in the Cyberneum of the Max Plank Institute for Biological Cybernetics, Tübingen. The image depicts a prototype of the mobile piezo belt. A laptop on the back controls HMD and the belt stimulation. Image taken from the project report of Ebert & Muil (2010).

6.2.7 Physiological Integration: Nystagmography

We test if the heading information provided by the belt can be integrated into human perception in the absence of attention, as predicted by the automated processing hypothesis. The pilot study could show that belt information can influence the vestibulo-ocular reflex (VOR). Nystagmography is a technique related to orientation in space. It investigates the stabilization of visual stimuli on the retina during head rotational movements. The vestibulo-ocular reflex compensates for head rotation around the vertical axis. During head rotation in one direction, the eyes move in the opposite direction of the head movement to stabilize the image on the retina. This slow phase is followed by a rapid movement of the eyes in the direction of the head movement to account for the limited range of eye-movements. This quick phase is labelled the vestibular nystagmus. However, due to the hydrodynamics of the vestibular organ, the signals indicating a rotation and the eye movements habituate during sustained rotation. In a lit environment visual information supplements the vestibular system and the habituation is largely reduced (Kandel, Schwartz, & Jessel, 2000). The belt indicates rotations without habituation. Hence the Automatic Processing Hypothesis predicts an increase of eye movements during body rotation and a decrease of eye-movement in the phase after stopping body rotation. We analyse belt-induced differences in the gain factor between eye- and chair velocity in the acceleration phase, as well as in belt-induced differences in the exponential decay in the nystagmus frequency after the acceleration/deacceleration phases.

6.2.8 Cortical Integration: Functional Magnetic Resonance Imaging (fMRI)

We use a recent path integration paradigm (Wolbers, Wiener, Mallot, & Büchel, 2007) to identify the cortical integration sites recruited by processing the information of the belt. Using our overall physiological measures of learning and behavioural utilization as regressors for strong learning effects allows to test the Correlation Hypothesis, i.e. that learning and behavioural utilization should increase with stronger cortical integration. Following the low-level processing hypothesis, physiological and psychological effects are mediated through part of the somatosensory topographic maps. By contrast, the high-level processing hypothesis predicts that behavioural utilization of the information relating to north requires integration in multimodal higher-level areas. In particular, according to the high-level processing hypothesis only subjects that establish the integration of the belt-stimulation into higher-level areas may report qualitative changes in sensory experiences that go beyond the tactile sensation proper.

6.2.8.1 fMRI Hypothesis

Sensory enhancement with new sensorimotor contingencies allows us to study the formation of a putative new sensory modality in the adult. Hence, the comparison of brain activity before and after training provides the rare opportunity to localize cortical areas related to a (new) modality without bias.

As in our behavioural experiments, we make use of a path integration paradigm because path integration is especially important in determining our position in space from polysensory cues during movement. Visual path-integration has especially been related to the medial superior temporal (MST) and ventral intraparietal (VIP) areas in the macaque, which can extract heading information from optic flow (Bremmer, Duhamel, Ben Hamed, & Graf, 2002; Duffy, Page, & Froehler, 2005). Head-direction cells in retrosplenial cortex also respond to visual input (Vann & Aggleton, 2004), and the heading information in turn affects place cells in the hippocampus (Etienne & Jeffery, 2004). The hippocampal complex has an established role as a polysensory locus of spatial orientation (Burgess, Jeffery, & O'Keefe, 1999; O'Keefe & Burgess, 1996; Spiers & Maguire, 2004). To name just one additional, non-visual modality, the hippocampus also receives major input from the vestibular system (Brandt et al., 2005; Save, Cressant, Thinus-Blanc, & Poucet, 1998). As in vision, vestibular input to the hippocampus involves the retrosplenial head-direction system, but also thalamo-cortical pathways (Russell, Horii, Smith, Darlington, & Bilkey, 2006). Hippocampal place cells are modulated by the activity of the animal in space, for instance by the speed of running (O'Keefe & Burgess, 1996), which further indicates a role in the computation of homing vectors, that is, of where we are in space. Yet the discovery of grid cells (Hafting, Fyhn, Molden, Moser, & Moser, 2005) and path cells (Jacobs, Kahana, Ekstrom, Mollison, & Fried, 2010) suggests that computation of spatial information might also be computed upstream of the hippocampus in structures of the entorhinal cortex. Ultimately, sub regions of prefrontal cortex have been suggested to hold an integrated spatial signal in working memory (Jones & Wilson, 2005; I. Lee & Kesner, 2003). Recently Wolbers, Wiener, Mallot, & Büchel (2007), used fMRI to demonstrate the contribution of the hippocampus, the medial prefrontal cortex, and the human motion complex (hMT+) during path integration in humans. In

consequence, we hypothesize that the orientation information of the belt might interact with respective neural sources in the path integration task of (Wolbers et al., 2007). In addition navigation strategies of route following and way finding have been linked to an areas know as HC+, involving the pterirrhinal cortex, and the caudatum (Hartley, Maguire, Spiers, & Burgess, 2003; Wolbers & Büchel, 2005). Furthermore, the “parahippocampal place area” (PPA) has been directly related to the encoding of new information about local scene layout (R. Epstein, Harris, Stanley, & Kanwisher, 1999). As a direct consequence, we expect interaction between processing of novel local spatial layouts in the PPA and the processing of the global spatial information about north contained in the belt sensorimotor contingencies. In addition, similar to the hippocampus, also the right superior temporal gyrus (rSTG) has recently been suggested as important polysensory locus of spatial processing in humans and non-human (Husain & Nachev, 2007; Karnath, Ferber, & Himmelbach, 2001; Karnath, 2001). The rSTG is most frequently and profoundly affected among all types of neglect, including pure forms of neglect, and transforms converging input from multiple modalities including the vestibular, auditory, neck proprioceptive and visual input into higher order spatial representations (Karnath & Dieterich, 2006). Interestingly, the rSTG seems to contribute especially to spatial processing with respect to the orientation of the body in space. Kahane, Hoffmann, Minotti, & Berthoz (2003) applied electrical stimulation specifically in the STG in patients with epilepsy and observed illusionary rotary sensations around the longitudinal axis. In consequence, the rSTG is a further candidate area for interaction between processing of the information about north and multisensory processing of (body-) orientation in space. Moreover posterior parietal areas have been related to the functional mapping of reference schemes (Heed, Beurze, Toni, Röder, & Medendorp, 2011), to tracking of route progressions (Nitz, 2006) and to self motion (Bremmer, Duhamel, Ben Hamed, & Graf, 2000), in which the belt signal might interaction given firm integration of the direction signal into spatial processing. Also the thalamus is involved in self-motion processing (Marlinski & McCrea, 2008) and the insular cortex has been related to ego-centric spatial processing in interaction with proprioceptive information from neck muscles (Bottini et al., 2001). Hence both areas are further candidate areas involved in spatial processing that may interact with the belt information. Other candidate areas that might potentially be affected by the belt signals include the (right) temporal parietal junction, which has been related to the maintenance of a coherent body image (Arzy, Thut, Mohr, Michel, & Blanke, 2006; Tsakiris, Costantini, & Haggard, 2008) under essential input from the vestibular system (Lenggenhager, Smith, & Blanke, 2006), as well as to a sense of ownership of body parts (Preester & Tsakiris, 2009), which might indicate that the belt information is firmly integrated into the body scheme. Posterior parietal areas have been related to tool use (Culham & Valyear, 2006) as another neuronal mode of using the belt signal in behaviour. Further, Premotor cortex (Schwartz, Moran, & Reina, 2004) and cerebellum have been linked to predicting the sensory consequences of action (Blakemore et al., 2001; Synofzik et al., 2008). The tactile nature of the belt signal should induce processing in primary and secondary somatosensory cortices (Del Gratta et al., 2000; Delgratta et al., 2002; Itomi, Kakigi, Hoshiyama, & Watanabe, 2001; Maldjian et al., 1999; Nakamura et al., 1998) and a processing of tactile motion in the human middle temporal/V5 complex (Hagen et al., 2002).

Area	Associated Function	Exemplary Publication
Hippocampus	Place Cells	(Burgess et al., 1999; O'Keefe & Burgess, 1996; Spiers & Maguire, 2004)
Entorhinal cortex	Grid Cells / Path Cells	(Hafting et al., 2005; Jacobs et al., 2010)
hMT+	Motion Processing	(Wolbers et al., 2007)
MST, VIP	Heading Direction From Optic Flow	(Bremmer et al., 2002)
Retrosplenial	Heading Direction from Vestibular Signals	(Vann & Aggleton, 2004)
rSTG	Polysensory Spatial Area	(Karnath & Dieterich, 2006)
rTPJ	Coherent Body Model in Space, Sense of Ownership, Vestibular Integration	(Arzy et al., 2006; Blanke et al., 2005; Lenggenhager et al., 2006; Preester & Tsakiris, 2009; Tsakiris et al., 2008)
Posterior parietal	Reference Schemes Mapping, Route Mapping, Self Motion, Tool Use	(Bremmer et al., 2000; Culham & Valyear, 2006; Heed et al., 2011; Nitz, 2006)
Insular	Vestibular Integration, Ego-Centric Space	(Bottini et al., 2001)
Caudatum, HC+ Pherirhinal cortex	Route Following, Way Finding	(Hartley et al., 2003; Wolbers & Büchel, 2005)
PPA	Local Scene Layout	(R. Epstein et al., 1999)
Premotor cortex	Sensory Predictions	(Schwartz et al., 2004)
Cerebellum	Predictions about Sensory Consequences of Action, Sense of Agency	(Blakemore et al., 2001; Synofzik et al., 2008)
Thalamus	Self-Motion	(Marlinski & McCrea, 2008)
MT/V5	Tactile Motion	(Hagen et al., 2002)
S1, S2	Early Tactile Processing	(Del Gratta et al., 2000; Delgratta et al., 2002; Itomi et al., 2001; Maldjian et al., 1999; Nakamura et al., 1998)

Table 6.2-1: Candidate Neuronal Sides of Integration of Belt Information

6.2.8.2 Setup

We will use the paradigm of Wolbers, Wiener, Mallot, & Büchel (2007) to assess brain areas of path integration modulated through information of the belt. In short, participants will passively travel along two legs of a triangle and point toward the starting location with a joystick. Instead of remembering the starting location, during control trials subjects will be asked to memorize the ego-centric direction of an arrow presented before the onset of the trial, and to point towards the direction of this arrow again in ego-centric coordinates after traveling along the second leg. That is, in the control condition subjects will experience identical visual and belt stimulation and also perform an identical motor task, but do not take the changes in the heading direction into account that are necessary in the homing condition.

As in the virtual reality experiments on multimodal integration, subjects will view a minimal visual environment from a first person perspective that provides only optic flow by a floor texture. However, as in (Wolbers et al., 2007), virtual motion will be passive to avoid confounding motor activations (by use of a joystick) and to ensure identical travel durations in each trial and subject. Eight outbound paths will be used both in the experimental conditions with correct belt information and without belt information and the control conditions. Paths will be comprised of one intermediate rotation and two translations. To ensure identical onsets of the translation period, the length of the first translation will be kept constant (at 8.5 m). Intermediate rotations differ in turning direction (left, right) and turning angle (30°, 60°, 90°, 120°). Since path integration in virtual environments is most accurate when displacement velocity resembles those of natural locomotion (Ellmore & McNaughton, 2004), a speed of moderate walking will be used for translation (maximum speed 2 m/s) and rotation (maximum speed 40°/s). Sequences of translation and rotation will follow the same trapezoid velocity profile with linear increases and decreases of velocity. The plateau of the trapezoid velocity profile will change according to the length of the translation or rotation angle. To keep total travel times constant over all trials, lengths of the second translation will be adjusted depending on the angle of the intermediate rotation, i.e. the second lag will be shorter for trials with longer rotations.

6.2.8.3 Training

To ensure that participants are familiar with the homing paradigm outside the scanner before scanning, fMRI measurements will be preceded by our behavioural experiments. Furthermore, to minimize learning effects during the scanning and specifically to train the usage of the belt in virtual navigation in a horizontal body position, participants will also receive training in virtual triangle completion in the horizontal body position outside the scanner before the actual measurements. These training sessions will use a different set of 8 training triangles, in which the length of the first leg is also kept constant at 8.5 m as in the fMRI triangles, but with different turning angles (45°, 75°, 105°, and 135°). Only during training trials will responses be followed by instant feedback, i.e. by providing an arrow that indicates the correct direction towards the origin.

6.2.8.4 Procedure

Immediately before the actual measurements, participants will receive one additional training session of 16 trials within the fMRI environment but without concurrent fMRI recording. This will be followed by an experimental session and a separate final control session. In the experimental session, each path will be repeated five times with and five times without the belt information in pseudo-randomized order and with control of sequential effects. This yields a total of 160 trials (80 experimental, 80 control). In the horizontal position, virtual north will arbitrarily but consistently be defined in a virtual “magnetic field” spanned perpendicularly to the longitudinal body axis, as in the vertical usage of the belt. During travels on outbound paths, the belt signal will continually be updated with respect to the direction of virtual north from the current position in the virtual space. To prepare subjects, each trial will start with a passive presentation of the virtual environment for 4s that indicates the condition, followed by the outward journey that always lasts 11.9 s. At the endpoint of the second translation, subjects will use an MR-compatible joystick to point toward the origin of the travel within a 5 s interval. Pointing responses will be recorded when joystick deflection exceeds a virtual circle corresponding to 80% of maximal deflection. During a 4s interval after the pointing response, subjects will be rotated back to the orientation towards virtual north at the beginning of the trial, such that all trials (with and without belt) start with the same orientation with respect to virtual north. This re-orientation will always be in the opposite direction than the turning through the trial (i.e. backward). As the temporal duration of backward-turning depends on the size of the absolute angular displacement, the virtual setup will be shown for the remaining time until the 4s window is completed. During intertrial intervals, a black screen will be presented randomly for 4 or 5 s. This yields a net scanning time of 40 minutes for the experimental and the control conditions, respectively.

Visual path integration involves both the processing of self-motion cues, as well as a working memory component for changes in distance and direction from the starting point. Hence, a control task is necessary that provides identical visual stimulation and motor responses, a working memory component unrelated to the path, as well as identical belt stimulation. In the final control session, subjects hence will travel along the same 40 paths as in the experiments. However, during the initial 4s starting period, an arrow will be presented in parallel to the ground plane, and subjects will be asked to remember its direction in an egocentric frame of reference, and then to pay attention to the outward journey. At the endpoint of the second translation, subjects will have to point into the direction of the arrow again in an egocentric reference frame, i.e. without taking into account the changes in heading throughout the travel.

With the belt, path integration additionally requires somato-sensory processing of the belt stimulus. Therefore subjects will perform the control condition with and without the belt. In this control condition the global orientation aspect of the belt signal is irrelevant for the task, but the purely tactile aspect of the belt signal is preserved.

Control tasks will deliberately be recorded in separate sessions to minimize the possibility that subjects engage in path integration during the control task. Yet it is possible that subjects do update their heading direction automatically. Then if the direction of the required pointing response (i.e. the direction of the arrow) differs from the direction of the homing vector to the starting location, this could potentially elicit a mismatch related activity. Hence to minimize this potentially confounding effect, in the control condition the required pointing direction of the arrow will always coincide with the homing vector toward the starting position. This design also allows

to completely match the distribution of required pointing responses between experimental and control trials.

In summary, control trials provide identical visual and somatosensory stimulation, a working memory component that is unrelated to the travel path, as well as an identical motor response, but do not require subjects to path integrate.

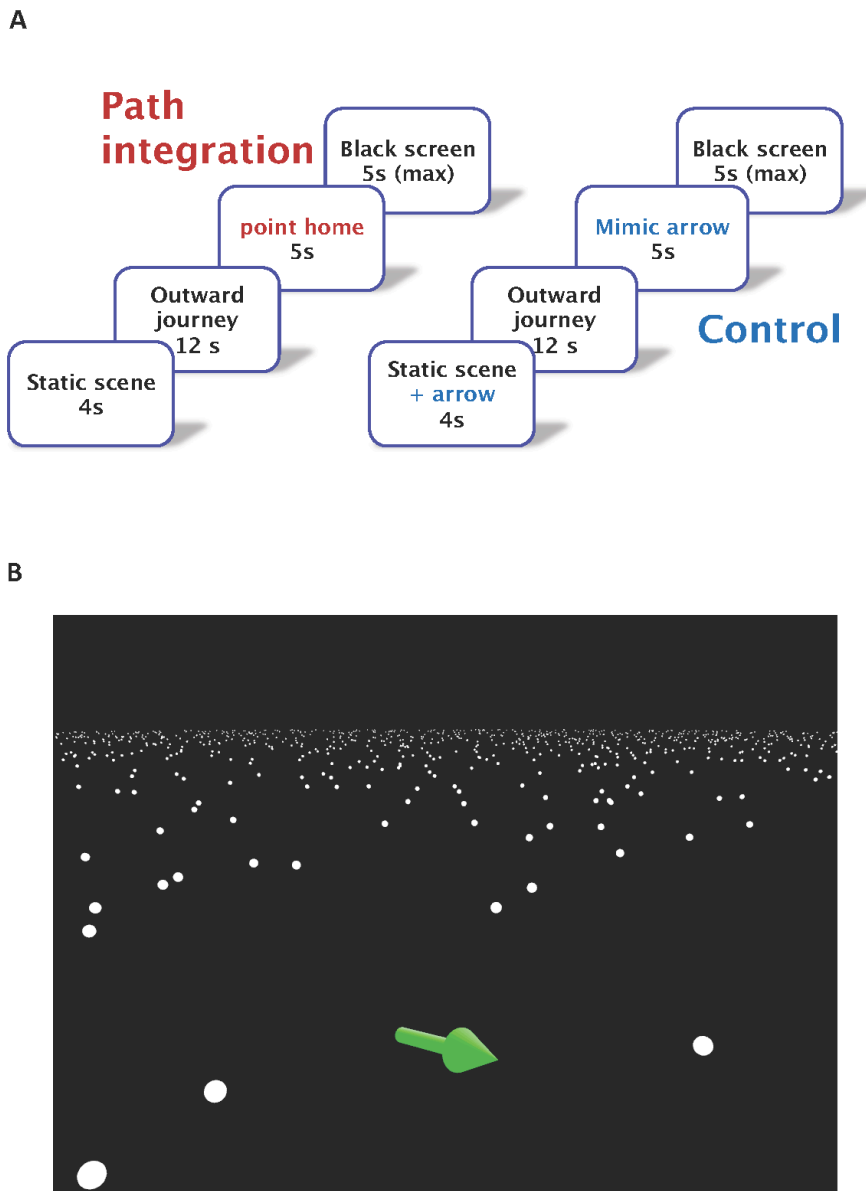


Figure 6-8: Design of fMRI Homing Paradigm.

(A) In the path integration condition, subjects are lead from a static scene on an outward journey and have to point to the starting point within a response interval. In a control conditions for optic flow and movement processing, subjects are asked to reproduce the direction of an arrow given prior to the outward journey instead of pointing home. (B) Minimal virtual environment with limited-lifetime dots. Subjects are asked to point using the green arrow. Figure B taken with permission from Johannes Keyzers' Bachelor Thesis.

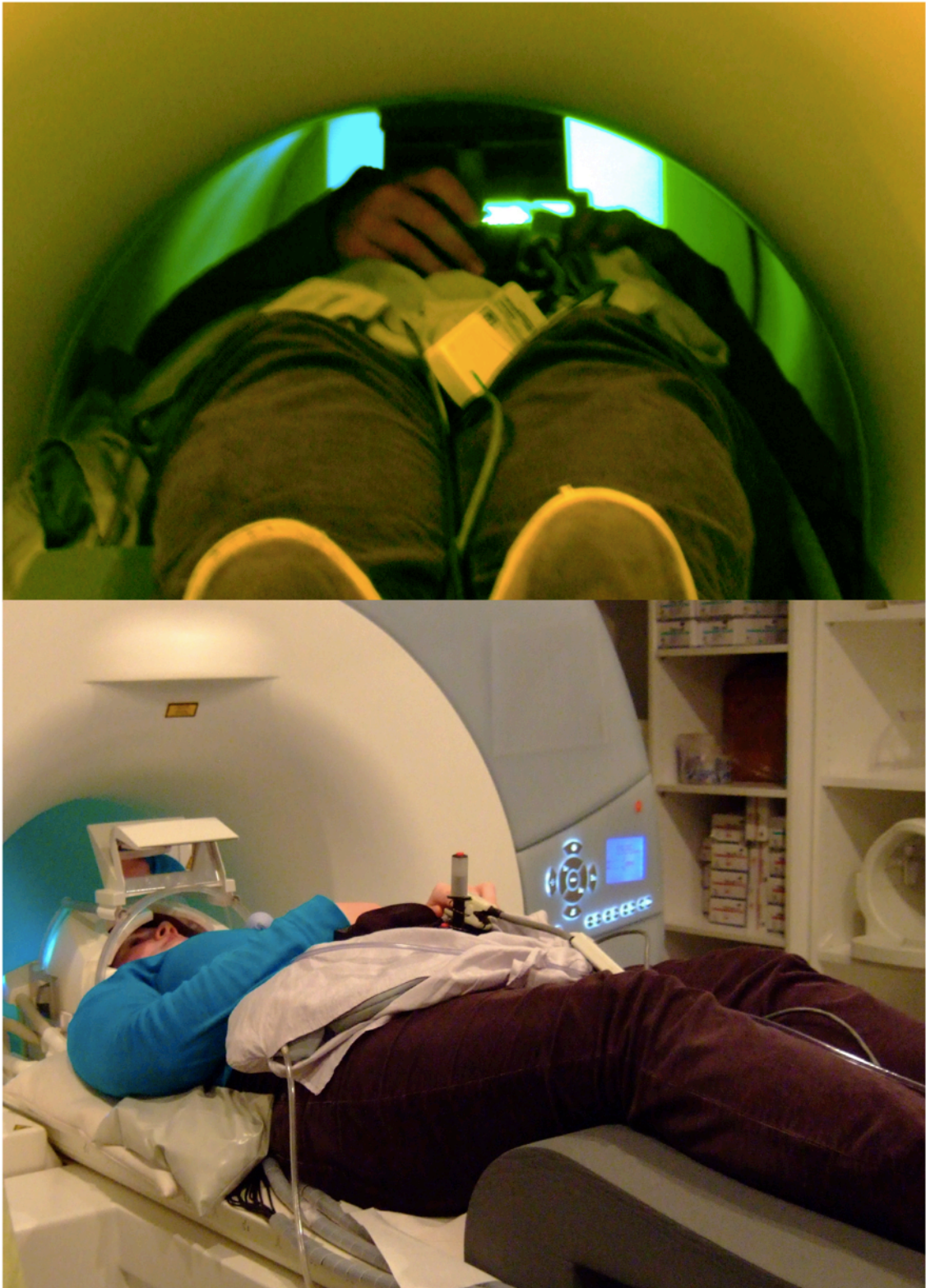


Figure 6-9: Complete feelSpace fMRI Setup

6.2.8.5 Analysis

After appropriate pre-processing, we will specify design matrixes containing four separate sessions (pre-training experimental and control, post-training experimental and control) to remove session specific effects. Triangle paths and pointing responses will be modelled as boxcar functions convolved with a hemodynamic response function (HRF). Trials in which participants fail to respond within the response interval of 5 s will be defined as separate regressor, which allows excluding them from analysis. Further regressors will be added for each turning angle (30°, 60°, 90°, 120°), collapsing left and right turning angles, and the belt condition (with, without).

Following our overall design, we analyse within-subjects performance to identify the neural sources recruited by path integration with the belt. We will add regressors in which the HRF of the path regressors, for both experimental and control sessions are parametrically modulated with the absolute pointing error on each trial. We add additional models for an overall habituation of the BOLD response across sessions. Specific effects will be tested with the appropriate linear contrasts of the parameter estimates, and the corresponding contrast images will subsequently be entered into a random effects analysis. We will test for main effects of the belt signal, of path integration, of training, as well as contrasts for the difference in path integration with and path integration without the belt after training and before training.

Furthermore, we can also follow the between-subjects analysis of Wolbers, Wiener, Mallot, & Büchel (2007) and decompose each participant's error into an overall bias (an overall tendency to undershoot or overshoot), random errors (fluctuations in response consistency) and systematic errors (in the individual ability to encode information about the pathway, as described in Wolbers, Wiener, Mallot, & Büchel, (2007). Between-subject multiple regression analysis then can identify the areas in which activation co-varies with each error type across subjects. Furthermore, it also allows identifying areas selectively engaged in with usage of the belt condition after training across subjects.

At last, we will analyse fMRI data in relation to behavioural, physiological and subjective measures of the applied project as between-subjects regressors. This allows testing the correlation hypothesis, in which local neuronal changes should be related to the degree of learning within a subject, as measured by a subject's degree of cortical plasticity during belt usage (sleep EEG), behavioural performance (homing), automatic processing (nystagmography), and subjective reports.

6.2.8.6 Regions of Interest (ROI)

To take into account our a priori hypothesis, for multiple comparison correction we supplement whole-brain analysis with an analysis of anatomical ROI. We define entire structures of the hippocampus, the endorhinal cortex, the superior medial frontal gyrus, S1 and S2 using the Wake Forest University Pickatlas (Maldjian, Laurienti, Kraft, & Burdette, 2003) and the anatomy toolbox of SPM (Eickhoff et al., 2005). As we are not aware of any precise definitions, we will create spherical volumes around previously reported coordinates of rSTG (Karnath, Fruhmann Berger, Küker, & Rorden, 2004), MST (Dukelow et al., 2001), VIP (Bremmer et al., 2001), retrosplenial cortex (Wolbers & Büchel, 2005). The PPA will be defined using functional localizer scans as regions in the posterior parahippocampal/collateral sulcus that correspond more strongly to scenes than to common objects (R. a Epstein, Parker, & Feiler, 2007).

6.2.8.7 fMRI Acquisition

Experiments will be performed with a 3-T scanner (Trio, Siemens AG, Munich, Germany) using a standard head coil and standard imaging parameters (e.g. Wolbers & Büchel, 2005; Wolbers, Weiller, & Büchel, 2004). Participants head will be immobilized with foam cushions to reduce movement. Foam cushions will also be provided under the lumbar spine and the thighs to rest participants without pressure on the back of the belt. Data will be analysed using SPM5 (www.fil.ion.ucl.ac.uk/spm). High-resolution structural MRI images will be acquired for each participant.

6.2.8.8 Voxel Based Morphometry

In addition to functional measurements, we will use voxel based morphometry (VBM) to identify structural plasticity due to usage of the belt information, as could be demonstrated for instance in the learning of sensorimotor tasks such as juggling, sensory discrimination training or meditation (Ashburner & Friston, 2000, 2001; Draganski & May, 2008; Driemeyer, Boyke, Gaser, Büchel, & May, 2008; Hölzel et al., 2008; Kwok et al., 2011; May & Gaser, 2006; May et al., 2007).

Two pre-treatment VBM measurements will be conducted prior to the experiment training phase to establish a stable baseline for comparison without random changes. As large changes are expected in the early training phase, an early VBM measurement after 3-5 days of training would be of high interest if applicable given the practical logistics in this ambitious project. The critical VBM measurement is conducted immediately after training and is optionally followed by a post-scan 6 months after training to show the development and decline of structural changes, respectively³⁴.

6.2.8.9 Conclusion

In conclusion, comparing the brain activity before and after training allows localizing the cortical processing of the stimulation by the belt. Sensory enhancement thus gives the unique ability to investigate the brain activity before and after learning of a (new) sensory modality. Following the low-level processing hypothesis, areas recruited by the belt information in processes of path-integration should be constrained to the primary modality, i.e. S1 and S2. Following the high-level processing hypothesis, path integration with the belt should recruit higher-level areas involved in spatial processing such as the hippocampal structure, entorhinal cortex, retrosplenial, rSTG, PPA, or the medial-prefrontal cortex. We can relate fMRI data to a subject's degree of learning, plasticity and change in subjective quality through belt usage. Since we learn a putatively new modality, this uniquely allows describing cortical changes related to the respective physiological and subjective changes.

³⁴ I am thankful to Arne May for discussions and feedback about the design of VBM measurements.

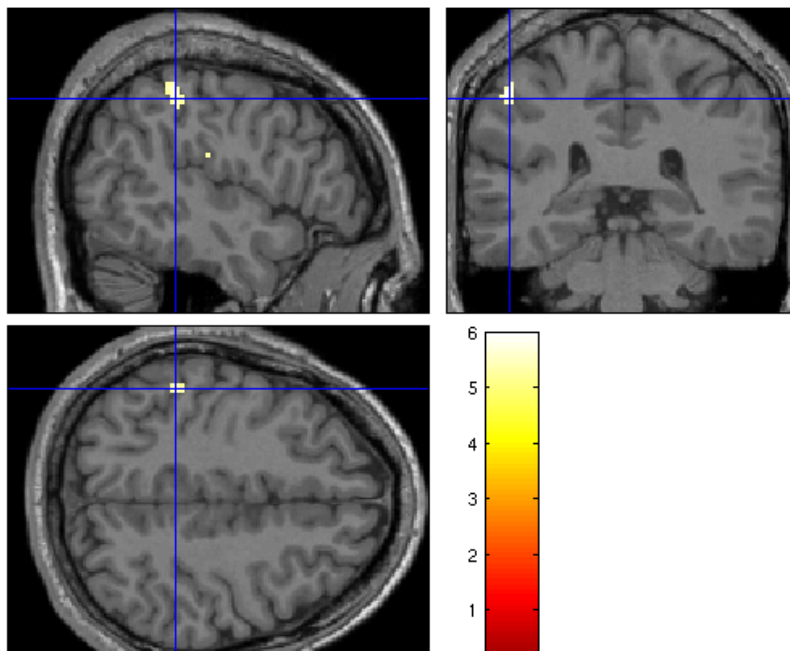
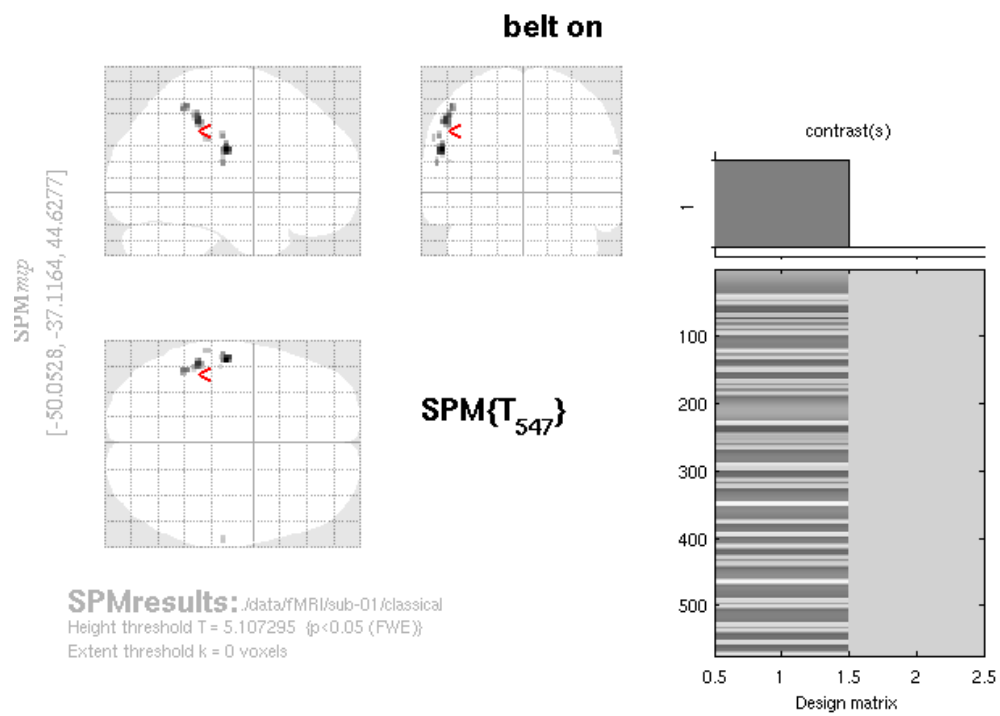


Figure 6-10: Preliminary Analysis of feelSpace fMRI Pilot Data.
 Shown is the contrast in the hemodynamic response between belt on / belt off conditions over the entire experiment at a family wise comparison error (FWE) of 0.05. This contrast isolates tactile processing of the belt signal.

6.2.9 Qualitative Experience: Subjective Methods to Describe the View From Within

Embodied theories of perception argue that perceptual awareness is established by mastery of sensorimotor contingencies. The new modality hypothesis predicts that after sufficient experience with the signals supplied by the belt during natural behaviour, a new quality of sensory experience will emerge. To study the sensory experiences of the subjects while wearing the belt, we have to take into account the private nature of perceptual experience.

There is a growing recognition in the consciousness sciences that private aspects of consciousness, such as the experience of using sensory substitution and enhancement devices, are only partially suited for third-person investigation but necessitate the application of rigorous methods for the acquisition of first- and second person data (Froese, Gould, & Barrett, 2011; Petitmengin, 2009; Varela & Shear, 1999).

We will take advantage of these recent developments and investigate the subjective quality as case reports using questionnaires, diaries, and through face-to-face interviews. We perform weekly interviews inspired by first- and second person methods for the acquisition of qualitative experience with subjects to cover all these aspects in depth. Upon completion of the training and finals tests we conduct comprehensive structured interviews.

The following describes Varela's general program of neurophenomenology, second- and first person techniques as well as the general qualitative data analysis approach of grounded theory for the context of research on sensory enhancement.

6.2.9.1 Neurophenomenology as Higher-Level Psychophysics

Neurophenomenology sets out to incorporate the first-person phenomenological and hermeneutic traditions of philosophical inquiry (Gallagher & Zahavi, 2006; Morley & Hunt, 2000) into modern cognitive science (Overgaard, Gallagher, & Ramsøy, 2008; Varela, 1996). In an important contribution, Varela and Shear (1999) argued that

- i. first-person experience cannot be derived from pure third-person data and is hence at least methodologically irreducible,
- ii. first- and third-person approaches should circulate in the program of naturalizing lived experience in a systematic and explicit manner
- iii. developing awareness to and reporting lived experience from the first person perspective is a skill that requires rigorous training and practice

The first two points are reminiscent to the relation between first- and third person investigation in the domain of psychophysics going back to Fechner (1860). Fechner instigated a novel trans-disciplinary research program to develop a scientific method that relates the phenomenal to the physical world and thus anticipated a principal goal of neuroscience (Ehrenstein & Ehrenstein, 1999). Measuring phenomenal perception has two foundational aspects in the psychophysical discussion: the problem of access and the problem of description. Psychophysics generally assumes that access to phenomenal experience is direct and not part of the problems encountered during measurement. The main concern of the psychophysical program is the problem

of description and the development of scientific tools of measurement to share experience in a consistent manner (ibid).

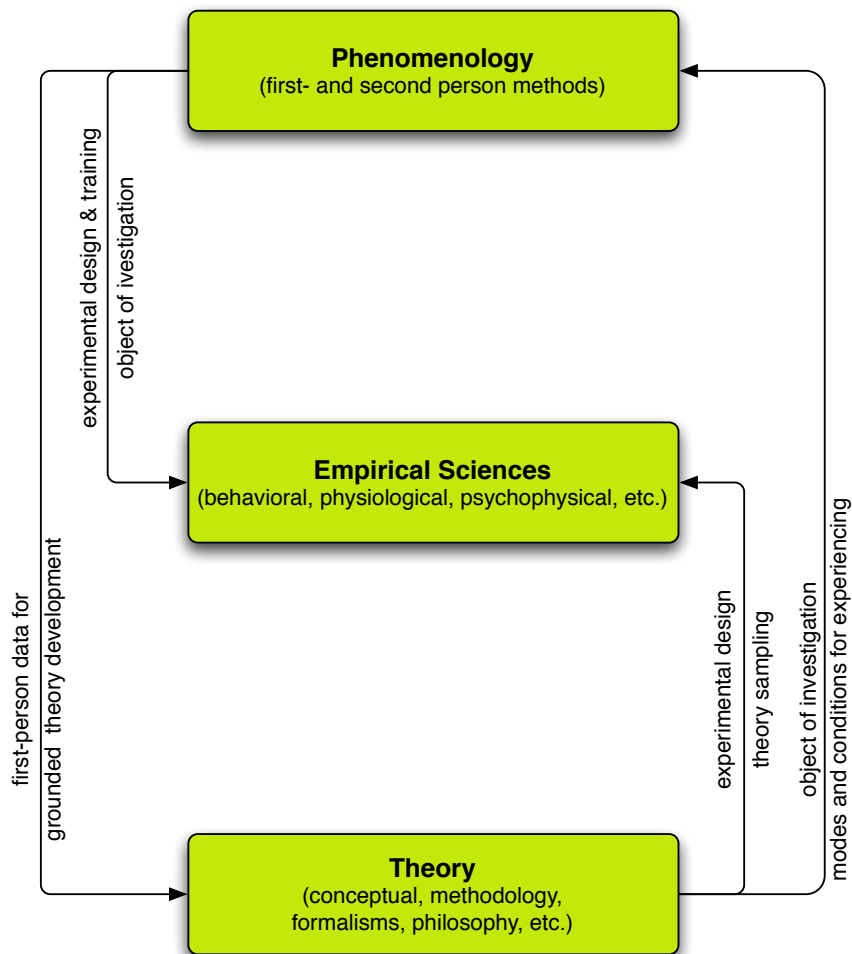


Figure 6-11: Circular Interaction in Neurophenomenology.
Adapted from Froese, Gould, & Barrett, 2011.

In contrast, the problem of access is an explicit part in the third point of Varela and Shear’s neurophenomenological proposal. While access to first-person content necessarily is direct once it occurs in the present, Varela & Shear draw on the phenomenological and Buddhist finding that becoming aware of subjective content, much like any other scientific method, is a skill that requires training. A major implication is that a scientific investigation of first-person experience requires substantial guidance and training for the observer and the scientist (Froese, Gould, et al., 2011). It is also “folk wisdom” within psychophysics that training of naïve observers yields more precise and valid psychophysical estimates (Blackwell, 1952; Green & Swets, 1964; Jäkel & Wichmann, 2006). A number of reasons additionally suggest a rigorous training of the scientist. First, neurophenomenology goes beyond psychophysics in the content of what is observed. Lived experience, unlike perception, is not conceptualized as a result of passive physiological stimulation that can be systematically varied on the third-person level and reduced to the psychophysical

methodology for instance of perceptual decisions in n-alternative forced choice tasks. Lived experience results from all processes of live. If it should be considered within the sciences of consciousness, training the scientist in becoming aware is a requirement for the development of first-second and third person methods and experiments for its investigation.

6.2.9.2 Explicitation Interview³⁵

Guiding observers through a process of becoming aware for scientific descriptions of subjective content is the main concern of the explicitation interview (EI) technique (Petitmengin, 2006; Vermersch, 2009). Verbal reports are always reminiscent and occur after the event and rely on short- or long-term memory of the situation. Spontaneous auto-noetic memories show that episodic memories can re-enact previous situations (Gardiner, 2001; Wheeler, Stuss, & Tulving, 1997), but in the context of prompted verbal reports, the memory of naïve observers is often abstract and in a summary form that is biased by top-down assumptions on what is being asked for by the situation. Explicitation interview is a non-suggestive protocol to guide observers into a state that yields verbal descriptions of the episodic memories of the experience itself.

The first step is to make contact with the situation by evoking episodic memory thereof. One lived experience occurs only in the singular of the present, and hence also authentic episodic memory of a situation is singular. EI guides observers to a singular chosen memory experience in the here and now of the interview situation. Nevertheless, lived experience occurs rapidly over time and with many sensations in parallel. Due to this complexity and the serial bottleneck of language, describing and experiencing are not concomitant. Memories must be continuously recalled in a state of evocation for the detailed description of concrete aspects. As episodic experiences are sensorial or emotional, the subject needs to make contact to the sensory and emotional dimension of the experience. Evocation states are signalled by observable aspects such as the use of co-verbal gestures that signal contact to bodily sensations or a concrete and specific language in the present tense that includes the use of “I” in association with a detailed vocabulary.

However, language interviews often prompt reports that entail knowledge or judgements or description of the context or goals involved in the experience. EI uses rephrasing and reinforcement techniques to guide observers from such satellite dimensions towards the concrete sensory memory of the situation. Repetition and rephrasing of what is being said reinforces a concrete language about the situation and creates a mode of concentration that animates subjects to give more of the echoed expression. Importantly, reformulation in contrast to a plain rejection of a subject’s satellite description yields a feeling of being understood. Combining reinforcement statements with subsequent questions allows to direct attention to concrete aspects of what has been uttered on the satellite aspect. Guiding questions can be synchronic and focus on a single point in time in parallel, or diachronic and focus on the sequential flow of events in the situation over time. For instance, if an object is named in a description, the interviewer could either ask about its size or colour, or alternatively about what happened before or after the object occurred. To avoid suggestive influences on the description, questions and guidance typically only repeat what has been said about the situation by the observers and take care to avoid the introduction of concrete knowledge or hypothesis about the situation on the part of the interviewer. Guidance

³⁵ I wish to thank Thi Bich Doan for her workshop on the Explicitation Interview technique at the Key Issues in Sensory Augmentation workshop at the University of Sussex, March 2009.

makes use of the indirect Ericksonian hypnotic language patterns (Petitmengin, 2006). To give an example, the beginning sequence of an interview might aim to guide subjects into a mode of concrete sensory observation of the present. Instead of explicit goal-directed instructing to start concentrating on the present, an instruction naïve subjects have difficulty to perform, indirect Ericksonian language might suggest that “if it feels right”, the subject “for a moment might recognize the contact of the body to the chair”, opening space for a non-volitional becoming aware of a sensory situation that is present even without the subjects explicit act of focused concentration. Alternatively, the interviewer may offer other contextualization’s, such as that “while parts of” the subject “remain busy with thoughts, another part may already have noticed if the body gives more pressure to the chair on the right or the left sit bones”. Again, the instruction aims for an open and non-volitional guidance of attention to what is present in sensation in concrete ways. However, unlike in this example, guiding attention to memories of the past that have not been witnessed by the scientist can not make use of his direct knowledge about the situation. Unless the scientist has first-person experience and can engage in a full second-person interview setting within a shared domain of reference, attention guidance will be restricted to the process of becoming aware of concrete aspects of the situation in general. Both scenarios give different weights on either the reliability or the validity of the interview.

Third, a main goal of explicitation interviews is to explicate pre-verbal reflexive and also non-reflexive experiences. Explicitation interviews respond to iconic, deictic or metaphoric gestures of the observer, asking to explicate the gesture via questions such as “what is opening like this?” or “what is separated in this way”. EI also states that it is possible to explicate pre-reflexive experience that have not been salient, i.e. that the subject has experienced without being aware of them, such as for instance the woman in the gorilla suit that escaped an observers perception in cases of inattentional blindness (Petitmengin et al., 2009).

EI requires prior training of the interviewer and at best a piloting of the interview itself. The methodology also provides a quasi-formal notation system to model the data obtained.

6.2.9.3 Focusing / Thinking-On-The-Edge³⁶

Following Gendlin’s epistemology of the implicit (Gendlin, 1962), the emergence of novel experiences is embodied and pre-verbal. Focusing is a methodology for a subsequent process of conceptualization and verbalisation of novel ideas (Gendlin, 2007; Hendricks, 2009). Reminiscent to the enactive mind-life continuity hypothesis (section 3.4.3), Gendlin argues that human epistemology occurs as a function of the full context of lived experience, including situational, bodily, emotional, sensory and perceptual aspects. Finding words for a situation is a process in which a bodily “Felt Sense” emerges in the present as soon as the verbal description found matches relevant aspects of the situation as judged by implicit epistemological processes. In contrast to EI, which focuses on explicating individual aspects of an experience in as much detail as possible, Focusing seeks to explicate the holistic whole of the situation.

Focusing offers many elements useful for a first-person science. Focusing aims to establish “presence”, a contact to experience that is characterized by open awareness, interest,

³⁶ I am thankful to Elmar Kruthoff’s workshop „Focusing – Die Zentralen Elemente“ at the interdisciplinary conference on „Leibgedächtnis & Therapy – Eine Begegnung zwischen Phänomenologie und Therapie“ at the University of Heidelberg, April 2011.

empathy and description rather than judgement. A state of presence is concrete, bodily and individual. Felt sensing is a process of identification with the present in which the observer at can know what an experience is (i.e. conceptualize and name) and at the same time continue to identify with how the experience is rather than to switch in perception to the description. Felt sensing of inner experiences is a mode of becoming aware that is independent of particular content and can hence be taught as a systematic skill, or guided by an experience interviewer. Similarly to EI, felt sensing is a mode of becoming aware that leads to a concrete language in the present tense. However, a particular concern of focusing is the conceptualization of situations that have not yet been transferred into proper words. Focusing interviews aid the transfer from the pre-verbal to the verbal by circling around aspects of a situation that can be delineated in the experience on a pre-verbal level and thus can be part of non-verbal thought (e.g. non-verbal comparisons, implications or associations) but not yet explicated in precise words. When trying to explicate pre-verbal thought observers frequently make anonymous deictic references in their language such as “this thing” or “that what I meant earlier”. Once established by the observer, the interviewer can use the same reference to relate back to this aspect of the situation. As in EI, the interviewer can guide attention of the observer by rephrasing and reinforcement of what has been said without prior knowledge of the situation. With first-person experience about the domain, the interviewer can also engage in a genuine second-person interview and use self-knowledge about similar situations to guide the interview.

Both latter aspects are useful methodological aspect for experiments on sensory enhancement. Focusing predicts that frequent and systematic use of anonymous referents accompanies the first verbal explications of genuinely novel experiences. Further, if available, first person experience of the interviewer can be used to guide observers to aspects of the sensory enhancement that may have escaped his attention. The interview then is no longer neutral, and feedback from the experience of the interviewer may be incorporated into training with the enhancement device. With such a second-person engagement with the observer over content, the scientific investigation can no longer unveil the results of unsupervised learning of with the device. However, if this is problematic for the scientific context depends on the question under investigation. Second-person person engagement does not necessarily render the observers experience untrustworthy, as long as, even thought developed with guidance beyond the process of becoming aware as such, they remain genuine experiences of the observer.

6.2.9.4 Awareness-Trough-Movement

The Awareness Through Movement (ATM) process offers a first person methodology for experiments on sensory enhancement. Awareness Trough Movement is applied in the context of non-verbal sensorimotor development (Feldenkrais, 2005; Ginsburg, 2010; R. Russel, 2004). It provides training of attention skills for the first-person exploration of the sensory consequences of movement in a kinaesthetic mode of action and perception. They key idea is to create a context in which observers detect or notice differences in perception resulting from self-initiated changes in actions. ATM can naturally be applied to the exploration of novel sensorimotor contingencies in sensory enhancement and will foster both training with the device as well as awareness of its changes to perception as both go hand in hand within an action-perception loop.

In a nutshell the general principle is to direct awareness for a systematic comparison of actual, self-initiated movements across conditions. On the sensory side conditions can be

established by guiding awareness to specific aspects of the sensory consequences of the movement, driven by hypothesis and prior experience or by what emerges as salient in the unfolding of the process. For instance, to become aware how specific body parts or global configurations participate in the movement, or to draw attention to the movement in an alternative frame of reference. On the motor side conditions for comparison can be established by changes in movement execution, for example by alterations of the body position or by the deliberate introduction of movement restrictions that block or reduce some movement options in order to render novel movement routes and their sensorimotor relations more salient.

Importantly, the purpose of the ATM process is not in the execution or training of movement as such but in the discriminations in sensory experience afforded by becoming aware of sensory consequences of movement. The methodology draws on the logarithmic nature of many psychophysical relations and trains skills to reduce the overall sensory load and motor effort in order to increase the just-noticeable-difference (JND). Based on phenomenology and theories of embodiment, the in perception the differences explored do not occur as purely sensory or motor differences but as the differentiation of contingencies in the sensorimotor loop with respect to both the origination of movement and its resulting perceptions. Hence ATM can aid mastery of a sensory enhancement device in its usage and in its perceptual effects.

Becoming aware in Awareness Trough Movement a skilled first-person process of directing attention while performing movements. It is not a verbal report technique but a method to become aware of current events in the present. An exciting option for sensory enhancement experiments is to combine first-person experiments in the present using ATM methodology with Explicitation Interviews for a scientific investigation of sensory enhancement. Instead of re-living a sensory enhancement experience from memory for its description in an interview situation, ATM provides a way of re-living the experience by experiments with the device in the present that could be guided by Explicitation Interview principles.

6.2.9.5 PRISMA

The PRISMA³⁷ method (Pieper & Clénin, 2010) is a practical-theoretical phenomenological research approach for studies of embodied intersubjectivity. Similar to Explicitation Interviews and Focusing, PRISMA is concerned with the explicitation of preverbal experience both for the development of skilled expertise as well as for a science of lived bodily experience. Similar to Focusing, PRISMA is based on the phenomenological notion of a lived body – “Leib” – (as opposed to just sub-personal somatosensory/kinaesthetic processes) in inter-subjective processes, and explicates Varela and Shears’ notion that the lived bodily experience of the scientist can and should be part of a science of consciousness as an object of study and as a source of experimental data (Varela & Shear, 1999). PRISMA relates to a “prismatic” uncovering of levels of analysis for inter-subjective experiences.

One domain concerns the perspective of the experience, namely a first person perspective to of oneself when engaging in a situation (self-perception), a second person perspective about

³⁷ PRISMA is collaborating with the 2012 Marie-Curie Initial Training Network, “TESIS: Towards an Embodied Science of InterSubjectivity” (FP7-PEOPLE-2010-ITN, 264828), <http://tesisnetwork.wordpress.com>, and the 2009 Marie-Curie Initial Training Network, “TESIS: Towards an Embodied Science of InterSubjectivity” (FP7-PEOPLE-2010-ITN, 264828), <http://tesisnetwork.wordpress.com>

another subject (perception of other) also engaging in the situation, and a third-person perspective (necessarily with intrinsic first-person components) when observing an inter-subjective exchange as an outside observer. In PRISMA first, second and third person perspectives are shifted, interlinked and varied in a consistent and re-traceable manner. The interactive situations investigated may consist of face-to-face interaction or of interactions recorded on video. Face-to-face situations are performed by a group of three protagonists at present and could also include the researchers themselves in a first-person approach. Also to analyse former interaction on video, investigators form an interactive research team of three. The video could also be a recorded version of a face-to-face situation already experienced. That means that within the prismatic process, inter-subjective episodes are embodied in all three roles - two agents and an observer - by each member of a group of three participants.

A second domain of PRISMA concerns the mode of experience elicited by the situation, namely a focus on sensorimotor impressions (sensing), emotional feeling, or thinking. PRISMA methodology provides a short notation system for each aspect as well as a systematics for analysing the data gained during the process.

With respect to sensory enhancement, PRISMA may be used in the context of intersubjective experimental settings. Intersubjective spatial tasks could be designed that either require usage of the directional information provided by the belt signal in inter-subjective ways, or allow communication about the task between participants. Video analysis may depict such belt related spatial episodes on video. Then the analysis can be performed with trained observers that have first-person experience with the belt signal, untrained naïve observers. One prediction is that observers with high confidence and training with the belt information will converge on more common notations in all level of analysis, in particular that they can engage more easily in a mode of sensing when describing common or video-displayed experiences with the belt. From the perspective of Focusing, such language may also contain episodes of searching for novel words or descriptions that can be clearly felt by observers, and which are content of a discourse, but initially only in vague and abstract terms. In Gendlin's epistemology, such episodes would serve as indicators for genuine novel experiences outside what is available in the common language and conceptual system before training. By contrast naïve PRISMA participants or video observers, without access to the belt information or insufficient training, should show more heterogeneous notes and a more abstract mode of experience.

6.2.9.6 Descriptive Experience Sampling

The primary focus of Descriptive Experience Sampling (DES) is on a random sampling of experience throughout everyday situations (Hurlburt & Akhter, 2006; Hurlburt & Heavey, 2001). Observers are provided with beepers that signal in random intervals and prompt a quick notation of the experience directly prior to the beep. Within 24h, the DES protocol conducts a follow-up interview to explicate the experience.

6.2.9.7 Grounded Theory

The neurophenomenological program poses a circularity between physiological experiments and lived experience for a science of consciousness (Froese, Gould, et al., 2011; Varela & Shear, 1999; Varela, 1996). Experiments and experience both provide objects of investigation and constraints for the other, and similarly phenomenological second-person

interview techniques exploit personal experience of the scientist in the process of becoming aware (Froese, Gould, et al., 2011).

Circularity between phenomenology, experiment and scientific interpretation is common to qualitative research methods. We use the standard qualitative approach of grounded theory (Charmaz, 2003; Glaser & Strauss, 2009) to investigate the subjective experience of sensory enhancement. Grounded theory specifies a systematic iterative qualitative data analysis approach to develop, test and revise theories from subjective data, from experiments, and from expert knowledge about the process under investigation. Grounded theory suggest a “theoretical sampling” by evaluating the processes of interest in detail in iterations of hypothesis-driven tests, mostly in the form of case studies. Hence grounded theory is a systematic way to derive at theories in a novel domain.

Broadly speaking, in grounded theory the analysis is equivalent with the writing of the documentation. The first step of the analysis is a line-by-line transcription of an interview to allow constant comparison between parts of the text. This step ignores context to focus on the data as much as possible. Albeit a transcription can never be a verbatim representation of the interview, we follow the natural approach to transcription (McLellan, MacQueen, & Neidig, 2003) and transcribe the spoken word as closely to natural speech as possible. We include mispronunciations and grammatical errors as spoken without correction, and also nonverbal sounds, pauses, filler words and background noises (McLellan et al., 2003). In particular Gendlin’s Focusing predicts that the search for a verbal description of novel experiences is accompanied by unspecific deictic references in the interview that need to be preserved for analysis. The second step conducts a focussed coding in which larger parts of the text are synthesized to drive hypothesis. These are then compared to the data by going back to the text on a line-by-line basis to modify first impressions. The third step seeks to derive categories of common themes and adds axial coding of sub dimensions of a category to the text. A fourth step uses theoretical sampling to obtain more data that validate or follow specific aspects of the interpretation. Typically, the analysis is presented in the form of a case study. It can be validated by comparison against the literature; by increasing the procedural reliability with standardized interview procedures, rules of coding and training of interviewers; by triangulation across different qualitative methods or researchers; by generalisation of the results to compare conditions or cases: or by predictions via theoretical sampling.

6.2.9.8 Subjective Methodology for Sensory Enhancement

The methodology in the current considers elements of Explicitation Interviews, Focusing, Awareness Trough Movement and Descriptive Experience Sampling within the general iterative scheme of grounded theory. Diaries and interviews in the pilot experiments (Nagel et al., 2005) as well as personal first-personal experience of project members revealed first aspects of the subjective experience related to the belt, which will form a basis for further interviews:

- ***Tidiness and sleepiness.*** Based on observations that sleep promotes plastic memory consolidation processes, we measure use-dependent activity changes in neural activity during sleep by means of sleep EEG recordings as a physiological quantification of learning. We also hypothesize that strong learning experiences with the belt are accompanied by a feeling of exhaustion and a larger subjective need of sleep, especially during the first days of training. Here, we asses subjective sleepiness via

self-reports like Karolinska Sleepiness Scale. An increased need of sleep should be an indicator of successful learning experiences, and KSS ratings have been seen to be a useful proxy for EEG or behavioural indicators of sleepiness (Kaida et al., 2006). (O’Keefe & Burgess, 1996; Spiers & Maguire, 2006)

- **Concentration and awareness.** The extent of effortful attention invoked when accessing the information provided by the belt is an indicator of the subjective engagement in the learning task, and initially may be a prerequisite for successful learning. However, with successful mastery, unattended and effortless usage of the belt indicates that the information of the belt can be processed automatically.
- **Spatial quality.** In the pilot study, some subjects reported an experience the environment as more orderly with intuitively available reference points that helped in the understanding of relations between places. This led to a subjective improvement in the ease of memorizing spatial relations, or in a switch from local clues to global navigation strategies. Some subjects felt the size of the spatial context to increase, and shrink back after they stopped wearing the belt. The reports of these subjects suggest that the sensation when wearing the belt reflected properties of the environment that go beyond the simple tactile stimulation. The high-level processing hypothesis predicts that qualitative changes in perception require multimodal, modality invariant processing. Hence, only subjects with increased high-level activity in fMRI should report about qualitative changes in their sensory experience.

Within the feelSpace Blind project (section 6.2.10), we developed a variant of DES and EI that will be further used also in the current project

- Subjects will be asked to file notes about their experience with the belt on a daily basis.
- We conduct weekly interviews that take elements from Explication Interview and Focusing to explicitate these experiences in detail.
- We also combine ATM with EI during training session, guiding the subject to perform navigation related movement with the belt while also guiding his awareness to the effect of the movement on his perception of space both in a first-person (i.e. within in his own awareness) and a second-person process (i.e. as verbal report).
- To obtain a random sampling of daily experiences, we plan to modify the DES methodology by replacing the beeper with random calls on a mobile phone followed by short Explication Interviews about the experience directly prior to the call.

6.2.9.9 Sense of Direction Scale

We will use the German version (Münzer & Hölscher, 2011) of the Santa Barbara sense of direction scale (SOD) (Hegarty, Richardson, Montello, Lovelace, & Subbiah, 2002) to assess the sense of direction of subjects before and after training in self-reports. The “global-egocentric-subscale” has been related to abilities for spatial updating of oneself in space during of self-motion

in environmental space, and also for the acquisition of spatial knowledge via learning through self-experience. A “survey-subscale” relates to processes of map formation. Most interestingly for the context of feelSpace, the “cardinal scale” is related to an absolute orientation by use of cardinal directions such as north or south (Münzer & Hölscher, 2011). All scales have been validated against respective behavioural data.

6.2.9.10 My First-Person Experiences with the feelSpace belt

I was frequently wearing various prototypes of the feelSpace for longer periods of time. My own first-person experience with the signal has been that:

- **At initial contact**, the belt stimulation felt like a purely tactile stimulation that moved counter-clock wise on the waist, i.e. an egocentric experience.
- **During later phases**, I infrequently experienced spontaneous episodes of being touched by “something” from the outside. This feeling shared some similarity with the feeling of leaning my back against the edge of an open door or the edge of a wall. Here the perceived position of the edge is stable in space, despite the physical changes in the tactile contact of edge with the skin. Similarly, in these sporadic periods the belt stimulation felt solid and stable in space and moved around the waist without moving in space, as if I was in some sense “leaning” against it. The episodes occurred only spontaneously, and they were rare. I had the immediate urge to “make” or hold this mode of perception, as in holding one version of an ambiguous figure such as the Neckar cube, however, I could voluntarily neither influence the occurrence nor the duration of such periods.

From the literature on spatial development (see section 3.3.2), these experiences suggest a beginning integration of the belt signal into an allocentric perception of space, switching back and forth between the initial egocentric and yet unstable allocentric mode of perceiving. This interpretation supports the new modality hypothesis, according to which the novel spatial information of the belt signal is recognized by the brain as a novel sensory source of information about space and experienced as a novel quality in perception. However, from this first-person data, the novel modality would occur at the level of the sense organ rather than at the level of the perception, on of the options suggested for the definition of a sensory modality (Auvray & Myin, 2009). This qualitative data suggests an integration of the tactile surface signal via its higher-order spatial information into established allocentric modes of spatial perception, leading to a switch from an ego-centric tactile perception on the body to a tactile perception that has a direction within space.

6.2.10 feelSpace Blind

A pilot study provided long-term sensory enhancement with directional information to an adult male congenitally blind subject for six weeks. We assessed the effects of training by pointing tasks in highly familiar and novel environments, a homing task, and subjective interviews.

Behavioural data and verbal reports indicate that the vibro-tactile directional signal showed no obvious immediate usefulness the navigational skill set of the congenitally blind subject. In fact, the spatial-directional interpretation of the tactile signal seemed not intuitively available to him based on his self-exploration of space during an initial unsupervised training period alone. On the first presentation, the directional signal even strongly distorted his naturally superior ability for homing in small spatial scales. However, in a novel large-scale environment, training with the sensory enhancement device allowed him to keep his orientation calibrated relative to a local external reference point, a navigational skill that is extremely difficult for him without the belt signal when no known auditory or tactile landmarks are available. We observed no improvement in pointing from multiple locations during the early beginning of the training period, consistent with a lack of intuitive spatial interpretation of the vibro-tactile direction signal. Yet after cognitive grounding of the directional aspect of the tactile signals by a verbal description of scene relations, pointing performance benefited substantially. Orientation was far superior compared to baseline not only for the points described verbally, but also for novel locations within the scene. Even without the belt some improvement was observed. Without any need for intervention, the subject discovered new spatial relations by himself in highly familiar environments based on the information of the belt. At no point did the subject report qualitative changes of spatial perception. However, an unnoticed mal-function of the compass during a longer, twisted walk at the end of the training period triggered the erroneous impression of an unusually long path leading straight ahead, to which he spontaneously commented on in surprise before noticing the belt malfunction.

In summary, after spatial grounding of the signal, this congenitally blind subject could stabilize the calibration of his orientation towards external reference points in a novel environment, and thereby improved pointing performance following a one-time explanation of scene layout. The results in the unsupervised training period are consistent with a spontaneous usage of the directional signal in an ego-centric route-based navigation strategy that many congenitally blind person's are hypothesized to favour over an allocentric cognitive mapping of space. However, the supervised training period showed the unique potential of the belt signal to train a cognitive mapping of novel environments given sufficient and systematic exploration of how the belt signal behaves in the particular environment. This suggests that the belt signal can compensate for the lack of spatial stability otherwise provided by vision, and thereby the potential to enhance the navigational skill set of congenitally blind persons towards allocentric strategies, given sufficient training. Erroneous spatial self-localisation caused by an inconsistent belt signal after training indicates that the belt signal can be integrated into everyday spatial experience, and that it can dominate the directional information given by the natural senses.

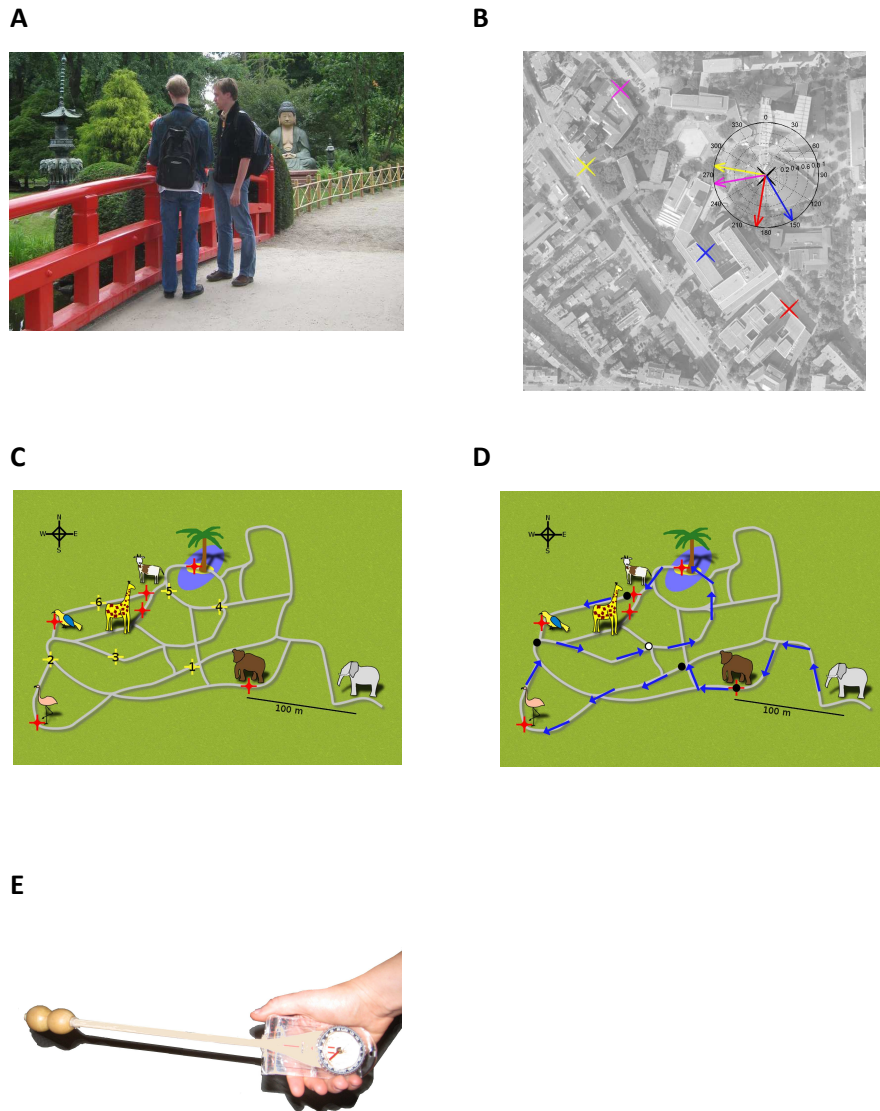


Figure 6-12: feelSpace Blind Pilot Study.

(A) Subject during training phase in Hamburg zoo. (B) Pointing locations in familiar environment. (C) Unfamiliar pointing locations in Hamburg zoo. (D) Test of orientation stability during a guided tour in the post training tests. Black dots indicate positions with stable orientation with respect to zoo layout. (F) Custom made pointing device. Figure adapted with permission from the Bachelors Thesis of Anna-Antonia Pape.

7 Declaration

I hereby confirm that I contributed significantly to all materials used in this thesis, and that I wrote this thesis independently and made no use of resources other than those indicated. This thesis has not been used, either in the same or different form, to fulfil any other examination requirements. This thesis was neither published in Germany nor abroad, except for the parts indicated above. Copyright of text and figures has been or will be transferred to the respective publishers.

Signature

8 References

- Abbott, L. F. (2008). Theoretical neuroscience rising. *Neuron*, *60*(3), 489–95.
doi:10.1016/j.neuron.2008.10.019
- Agre, P. E. (1997). *Computation and human experience*. New York: Cambridge University Press.
- Amedi, A., Floel, A., Knecht, S., Zohary, E., & Cohen, L. G. (2004). Transcranial magnetic stimulation of the occipital pole interferes with verbal processing in blind subjects. *Nature neuroscience*, *7*(11), 1266–70. doi:10.1038/nn1328
- Amedi, A., Raz, N., Pianka, P., Malach, R., & Zohary, E. (2003). Early “visual” cortex activation correlates with superior verbal memory performance in the blind. *Nature Neuroscience*, *6*(7), 758–766.
- Andersen, R. a, Snyder, L. H., Bradley, D. C., & Xing, J. (1997). Multimodal representation of space in the posterior parietal cortex and its use in planning movements. *Annual review of neuroscience*, *20*, 303–30. doi:10.1146/annurev.neuro.20.1.303
- Anderson, M. L. (2003). Embodied Cognition: A field guide. *Artificial Intelligence*, *149*(1), 91–130.
doi:10.1016/S0004-3702(03)00054-7
- Anderson, M. L. (2008). Circuit sharing and the implementation of intelligent systems. *Connection Science*, *20*(4), 239–251. doi:10.1080/09540090802413202
- Anderson, M. L. (2010). Neural reuse: a fundamental organizational principle of the brain. *The Behavioral and brain sciences*, *33*(4), 245–66; discussion 266–313. doi:10.1017/S0140525X10000853
- Angelaki, D. E., & Cullen, K. E. (2008). Vestibular system: the many facets of a multimodal sense. *Annual review of neuroscience*, *31*, 125–50. doi:10.1146/annurev.neuro.31.060407.125555
- Arzy, S., Thut, G., Mohr, C., Michel, C. M., & Blanke, O. (2006). Neural basis of embodiment: distinct contributions of temporoparietal junction and extrastriate body area. *The Journal of neuroscience : the official journal of the Society for Neuroscience*, *26*(31), 8074–81. doi:10.1523/JNEUROSCI.0745-06.2006
- Ashburner, J., & Friston, K. J. (2000). Voxel-Based Morphometry—The Methods. *Statistics*, *821*, 805–821.
doi:10.1006/nimg.2000.0582
- Ashburner, J., & Friston, K. J. (2001). Why voxel-based morphometry should be used. *NeuroImage*, *14*(6), 1238–43. doi:10.1006/nimg.2001.0961
- Auvray, M., Hanneton, S., & O’Regan, J. K. (2007). Learning to perceive with a visuo – auditory substitution system: Localisation and object recognition with “The vOICE”. *Perception*, *36*(3), 416–430. doi:10.1068/p5631
- Auvray, M., Lenay, C., & Stewart, J. (2009). Perceptual interactions in a minimalist virtual environment. *New Ideas in Psychology*, *27*(1), 32–47. doi:10.1016/j.newideapsych.2007.12.002
- Auvray, M., & Myin, E. (2009). Perception With Compensatory Devices: From Sensory Substitution to Sensorimotor Extension. *Cognitive Science*, *33*(6), 1036–1058. doi:10.1111/j.1551-6709.2009.01040.x
- Bach-y-Rita, P. (1972). *Brain Mechanisms in Sensory Substitution*. New York: Academia.
- Bach-y-Rita, P. (2004). Tactile sensory substitution studies. *Annals of the New York Academy of Sciences*, *1013*, 83–91.
- Bach-y-Rita, P., & Kercel, S. W. (2003). Sensory substitution and the human–machine interface. *Trends in Cognitive Sciences*, *7*(12), 541–546. doi:10.1016/j.tics.2003.10.013
- Ballard, D. H. (2009). Active Perception. *Encyclopedia of Neuroscience*. Elsevier. doi:10.1016/B978-008045046-9.01436-4
- Ballard, D. H., Hayhoe, M. M., Pook, P. K., & Rao, R. P. N. (1997). Deictic codes for the embodiment of cognition. *Behavioral and Brain Sciences*, 723–767.
- Barlow, H. (1953). Summation and inhibition in the frog’s retina. *The Journal of physiology*, *119*(1), 69–88.
- Barlow, H. (1961). Possible principles underlying the transformations of sensory messages. In W. Rosenblith (Ed.), *Sensory Communication* (pp. 217–234). Cambridge, MA: MIT Press.
- Barsalou, L. W. (1999). Perceptual symbol systems. *The Behavioral and brain sciences*, *22*(4), 577–609; discussion 610–60.
- Barsalou, L. W. (2008). Grounded cognition. *Annual review of psychology*, *59*, 617–45.
doi:10.1146/annurev.psych.59.103006.093639

- Barsalou, L. W. (2010). Grounded Cognition: Past, Present, and Future. *Topics in Cognitive Science*, 2(4), 716–724. doi:10.1111/j.1756-8765.2010.01115.x
- Bechtel, W. (1988). *Philosophy of Science: An Overview for Cognitive Science*. Hillsdale, NJ: Lawrence Erlbaum Associates.
- Beer, R. (2000). Dynamical approaches to cognitive science. *Trends in cognitive sciences*, 4(3), 91–99.
- Bell, M., & Fox, N. (1996). Crawling experience is related to changes in cortical organization during infancy: evidence from EEG coherence. *Developmental psychobiology*, 29(7), 551–61. doi:10.1002/(SICI)1098-2302(199611)29:7<551::AID-DEV1>3.0.CO;2-T
- Bell, & Sejnowski, T. J. (1997). The “independent components” of natural scenes are edge filters. *Vision research*, 37(23), 3327–38.
- Blackwell, H. R. (1952). Studies of psychophysical methods for measuring visual thresholds. *Journal of the Optical Society of America*, 42(9), 606–16.
- Blakemore, S. J., Frith, C. D., & Wolpert, D. M. (2001). The cerebellum is involved in predicting the sensory consequences of action. *Neuroreport*, 12, 1879–1884.
- Blakemore, S. J., Wolpert, D. M., & Frith, C. D. (1998). Central cancellation of self-produced tickle sensation. *Nature neuroscience*, 1(7), 635–40. doi:10.1038/2870
- Blakemore, S. J., Wolpert, D. M., & Frith, C. D. (2002). Abnormalities in the awareness of action. *Trends in cognitive sciences*, 6(6), 237–242.
- Blanke, O., Mohr, C., Michel, C. M., Pascual-Leone, A., Brugger, P., Seeck, M., Landis, T., et al. (2005). Linking out-of-body experience and self processing to mental own-body imagery at the temporoparietal junction. *The Journal of neuroscience : the official journal of the Society for Neuroscience*, 25(3), 550–7. doi:10.1523/JNEUROSCI.2612-04.2005
- Bliss, T. V., & Lomo, T. (1970). Plasticity in a monosynaptic cortical pathway. *The Journal of physiology*, 207(2), 61P.
- Boden, M. (2006). *Mind as Machine: A History of Cognitive Science*. Oxford University Press.
- Bottini, G., Karnath, H. O., Vallar, G., Sterzi, R., Frith, C. D., Frackowiak, R. S. J., & Paulesu, E. (2001). Cerebral representations for egocentric space: Functional-anatomical evidence from caloric vestibular stimulation and neck vibration. *Brain : a journal of neurology*, 124(Pt 6), 1182–96.
- Brandt, T., Schautzer, F., Hamilton, D. A., Brüning, R., Markowitsch, H. J., Kalla, R., Darlington, C. L., et al. (2005). Vestibular loss causes hippocampal atrophy and impaired spatial memory in humans. *Brain : a journal of neurology*, 128(Pt 11), 2732–41. doi:10.1093/brain/awh617
- Bremmer, F., Duhamel, J. R., Ben Hamed, S., & Graf, W. (2000). Stages of self-motion processing in primate posterior parietal cortex. *International review of neurobiology*, 44(12), 173–98.
- Bremmer, F., Duhamel, J.-R., Ben Hamed, S., & Graf, W. (2002). Heading encoding in the macaque ventral intraparietal area (VIP). *European Journal of Neuroscience*, 16(8), 1554–1568. doi:10.1046/j.1460-9568.2002.02207.x
- Bremmer, F., Schlack, A., Shah, N. J., Zafiris, O., Kubischik, M., Hoffmann, K., Zilles, K., et al. (2001). Polymodal motion processing in posterior parietal and premotor cortex: a human fMRI study strongly implies equivalencies between humans and monkeys. *Neuron*, 29(1), 287–96.
- Brentano, F. (1874). *Psychologie vom empirischen Standpunkt. Erster Band*. Hamburg: Meiner.
- Broadbent, D. (1958). *Perception and Communication*. London: Pergamon Press.
- Brooks, R. A. (1991). Intelligence without representation. *Artificial Intelligence*, 47(1-3), 139–159. doi:10.1016/0004-3702(91)90053-M
- Bubic, A., Von Cramon, D. Y. Y., & Schubotz, R. I. R. I. (2010). Prediction, cognition and the brain. *Frontiers in human neuroscience*, 4(March), 25. doi:10.3389/fnhum.2010.00025
- Buonomano, D. V., & Merzenich, M. M. (1998). Cortical plasticity: from synapses to maps. *Annual review of neuroscience*, 21, 149–86. doi:10.1146/annurev.neuro.21.1.149
- Burgess, N., Jeffery, K. J., & O’Keefe, J. (1999). *The Hippocampal and Parietal Foundations of Spatial Cognition*. Oxford University Press.
- Buswell, G. T. (1935). *How people look at pictures: a study of the psychology and perception in art*. Chicago University of Chicago Press (p. 198). Univ. Chicago Press.
- Buzsáki, G. (2004). Large-scale recording of neuronal ensembles. *Nature neuroscience*, 7(5), 446–51. doi:10.1038/nn1233
- Büchel, C. (1998). Functional neuroimaging studies of Braille reading: cross-modal reorganization and its implications. *Brain : a journal of neurology*, 121 (Pt 7, 1193–4.
- Büchel, C., Price, C., Frackowiak, R. S., & Friston, K. (1998). Different activation patterns in the visual cortex of late and congenitally blind subjects. *Brain: a journal of neurology*, 121 (Pt 3, 409–19.

- Campbell, F. W., & Maffei, L. (1974). Contrast and spatial frequency. *Scientific American*, 231(5), 106–14.
- Cassinelli, A., Reynolds, C., & Ishikawa, M. (2006). Augmenting spatial awareness with Haptic Radar. 2006 10th IEEE International Symposium on Wearable Computers (pp. 61–64). IEEE. doi:10.1109/ISWC.2006.286344
- Cerf, M., Harel, J., Einhäuser, W., & Koch, C. (2008). Predicting human gaze using low-level saliency combined with face detection. In J. C. Platt, D. Koller, Y. Singer, & S. Roweis (Eds.), *Advances in neural information processing systems* (pp. 1–8). Cambridge, MA: MIT Press.
- Chalmers, D. J. (1995). Facing Up to the Problem of Consciousness. *Journal of Consciousness Studies*, 2(3), 1–27.
- Chalmers, D. J. (1996). *The Conscious Mind: In Search of a Fundamental Theory*. New York: Oxford University Press.
- Charmaz, K. (2003). Grounded Theory: Objectivist and Constructivist Methods. In N. K. Denzin & Y. S. Lincoln (Eds.), *Strategies of Qualitative Inquiry*. London: Sage Publications.
- Cherry, E. C. (1953). Some Experiments on the Recognition of Speech, with One and with Two Ears. *The Journal of the Acoustical Society of America*, 25(5), 975. doi:10.1121/1.1907229
- Chklovskii, D. B., & Koulakov, A. a. (2004). Maps in the brain: what can we learn from them? *Annual review of neuroscience*, 27(Mitchison 1991), 369–92. doi:10.1146/annurev.neuro.27.070203.144226
- Chomsky, N. (1965). *Aspects of the Theory of Syntax*. MIT Press.
- Churchland, M. M., Yu, B. M., Sahani, M., & Shenoy, K. V. (2007). Techniques for extracting single-trial activity patterns from large-scale neural recordings. *Current opinion in neurobiology*, 17(5), 609–18. doi:10.1016/j.conb.2007.11.001
- Clancey, W. J. (1997). *Situated Cognition*. New York: Cambridge University Press. doi:10.2277/0521448719
- Clark, A. (1997). *Being there. Putting Brain, Body and World together again*. Cambridge, MA: MIT Press.
- Clark, A. (2006). Vision as dance? Three challenges for sensorimotor contingency theory. *Psyche*, 1–10.
- Clark, A. (2012). Whatever Next ? Predictive Brains, Situated Agents, and the Future of Cognitive Science. *Behavioral and Brain Sciences*, 1–86.
- Clark, A., & Chalmers, D. (1998). The extended mind. *Analysis*.
- Cohen, L. G., Celnik, P., Pascual-Leone, a, Corwell, B., Falz, L., Dambrosia, J., Honda, M., et al. (1997). Functional relevance of cross-modal plasticity in blind humans. *Nature*, 389(6647), 180–3. doi:10.1038/38278
- Collignon, O., Lassonde, M., Lepore, F., Bastien, D., & Veraart, C. (2007). Functional cerebral reorganization for auditory spatial processing and auditory substitution of vision in early blind subjects. *Cerebral cortex (New York, N.Y. : 1991)*, 17(2), 457–65. doi:10.1093/cercor/bhj162
- Colombetti, G. (2010). Enaction, sense-making and emotion. In J. Stewart, O. Gapenne, & E. Di Paolo (Eds.), *Enaction: Towards a New Paradigm for Cognitive Science*. Cambridge, MA: MIT Press.
- Colombetti, G., & Thompson, E. (2007). The feeling body: toward an enactive approach to emotion 3. In W. F. Overton, U. Müller, & J. Newman (Eds.), *Body in Mind, Mind in Body: Developmental Perspectives on Embodiment and Consciousness* (pp. 45–68). Lawrence Erlbaum Associates.
- Cosmelli, D. (2009). Attending to the Stream of Consciousness – A Methodological Challenge. In F. Aboitiz & D. Cosmelli (Eds.), *From Attention to Goal-Directed Behavior* (pp. 83–103). Springer.
- Crapse, T. B., & Sommer, M. A. (2008). Corollary discharge across the animal kingdom. *Nature reviews. Neuroscience*, 9(8), 587–600. doi:10.1038/nrn2457
- Culham, J. C., & Valyear, K. F. (2006). Human parietal cortex in action. *Current opinion in neurobiology*, 16(2), 205–12. doi:10.1016/j.conb.2006.03.005
- Dan, Y., Atick, J. J., & Reid, R. C. (1996). Efficient coding of natural scenes in the lateral geniculate nucleus: experimental test of a computational theory. *The Journal of neuroscience : the official journal of the Society for Neuroscience*, 16(10), 3351–62.
- Daniel, P. M., & Whitteridge, D. (1961). The representation of the visual field on the cerebral cortex in monkeys. *The Journal of physiology*, 159, 203–21.
- Debener, S., Ullsperger, M., Siegel, M., & Engel, A. K. (2007). Towards single-trial analysis in cognitive brain research. *Trends in cognitive sciences*, 11(12), 502–3. doi:10.1016/j.tics.2007.09.005
- Del Gratta, C., Della Penna, S., Tartaro, A., Ferretti, A., Torquati, K., Bonomo, L., Romani, G. L. L., et al. (2000). Topographic organization of the human primary and secondary somatosensory areas: an fMRI study. *Neuroreport*, 11(9), 2035–43.
- Delgratta, C., Dellapenna, S., Ferretti, A., Franciotti, R., Pizella, V., Tartaro, A., Torquati, K., et al. (2002). Topographic Organization of the Human Primary and Secondary Somatosensory Cortices:

- Comparison of fMRI and MEG Findings. *NeuroImage*, 17(3), 1373–1383.
doi:10.1006/nimg.2002.1253
- Desmurget, M., & Grafton, S. (2000). Forward modeling allows feedback control for fast reaching movements. *Trends in cognitive sciences*, 4(11), 423–431.
- Deutsch, D., & Deutsch, J. A. (1963). Attention: Some theoretical considerations. *Psychological review*, 70(3), 80–90.
- Dewey, J. (1896). The reflex arc concept in psychology. *Psychological Review*, 3(4), 357–370.
doi:10.1037/h0070405
- Di Paolo, E. (2006). Autopoiesis, Adaptivity, Teleology, Agency. *Phenomenology and the Cognitive Sciences*, 4(4), 429–452. doi:10.1007/s11097-005-9002-y
- Di Paolo, E. (2008). Extended Life. *Topoi*, 28(1), 9–21. doi:10.1007/s11245-008-9042-3
- Di Paolo, E., & Iizuka, H. (2008). How (not) to model autonomous behaviour. *Bio Systems*, 91(2), 409–23.
doi:10.1016/j.biosystems.2007.05.016
- Di Paolo, E., Rohde, M., & Iizuka, H. (2008). Sensitivity to social contingency or stability of interaction? Modelling the dynamics of perceptual crossing. *New Ideas in Psychology*, 26(2), 278–294.
doi:10.1016/j.newideapsych.2007.07.006
- Di Paolo, E., Rohde, M., & Jaegher, H. De. (2010). Horizons for the Enactive Mind : Values , Social Interaction , and Play Horizons for the Enactive Mind : Values , Social. In J. Stewart, O. Gapenne, & E. A. Di Paolo (Eds.), *Enaction: Towards a New Paradigm for Cognitive Science*. Cambridge, MA: MIT Press.
- Diedrichsen, J., Shadmehr, R., & Ivry, R. B. (2010). The coordination of movement: optimal feedback control and beyond. *Trends in cognitive sciences*, 14(1), 31–9. doi:10.1016/j.tics.2009.11.004
- Draganski, B., & May, A. (2008). Training-induced structural changes in the adult human brain. *Behavioural brain research*, 192(1), 137–42. doi:10.1016/j.bbr.2008.02.015
- Dreyfus. (1988). Making a mind versus modeling the brain: artificial intelligence back at a branchpoint. (S. R. Graubard, Ed.) *Daedalus*, 117(1), 15–43.
- Driemeyer, J., Boyke, J., Gaser, C., Büchel, C., & May, A. (2008). Changes in gray matter induced by learning--revisited. *PLoS ONE*, 3(7), e2669. doi:10.1371/journal.pone.0002669
- Duffy, C. J., Page, W. K., & Froehler, M. T. (2005). Head direction cells and the neural mechanisms of spatial orientation. In J.M. Wiener & J. S. Taube (Eds.), *Head direction cells and the neural mechanisms of spatial orientation* (pp. 319–345). Cambridge, MA: MIT.
- Dukelow, S. P., Desouza, J. F. X., Culham, J. C., Van den Berg, A. V, Menon, R. S., & Vilis, T. (2001). Distinguishing subregions of the human MT+ complex using visual fields and pursuit eye movements. *Journal of neurophysiology*, 86(4), 1991–2000.
- Dupuy, J. P. (2009). *On the Origins of Cognitive Science: The Mechanization of Mind*. Cambridge, MA: MIT Press.
- Ebert, M., & Muil, R. (2010). *feelSpace II - Report of a Study Project*. University of Osnabrück.
- Ehrenstein, W. H., & Ehrenstein, A. (1999). Psychophysical Methods. In U. Windhorst & H. Johansson (Eds.), *Modern Techniques in Neuroscience Research* (pp. 1211–1241). Berlin: Springer.
- Eickhoff, S. B., Stephan, K. E., Mohlberg, H., Grefkes, C., Fink, G. R., Amunts, K., & Zilles, K. (2005). A new SPM toolbox for combining probabilistic cytoarchitectonic maps and functional imaging data. *NeuroImage*, 25(4), 1325–35. doi:10.1016/j.neuroimage.2004.12.034
- Einhäuser, W., & König, P. (2003). Does luminance-contrast contribute to a saliency map for overt visual attention? *European Journal of Neuroscience*, 17(5), 1089–1097. doi:10.1046/j.1460-9568.2003.02508.x
- Einhäuser, W., & König, P. (2010). Getting real-sensory processing of natural stimuli. *Current opinion in neurobiology*, 20(3), 389–95. doi:10.1016/j.conb.2010.03.010
- Einhäuser, W., Rutishauser, U., & Koch, C. (2008). Task-demands can immediately reverse the effects of sensory-driven saliency in complex visual stimuli. *Journal of vision*, 8(2), 2.1–19. doi:10.1167/8.2.2
- Elbert, T., Junghöfer, M., Scholz, B., & Schneider, S. (1995). The separation of overlapping neuromagnetic sources in first and second somatosensory cortices. *Brain topography*, 7(4), 275–82.
doi:10.1007/BF01195253
- Ellmore, T. M., & McNaughton, B. L. (2004). Human Path Integration by Optic Flow. *Spatial Cognition & Computation*, 4(3), 255–272. doi:10.1207/s15427633scc0403_3
- Engel, A. K. (2011). Directive minds: How dynamics shape cognition. In O. G. and E. A. D. P. J. Stewart (Ed.), *Enaction: Towards a New Paradigm for Cognitive Science* (pp. 219 – 243). Cambridge, MA: MIT Press.

- Engel, A. K., Fries, P., & Singer, W. (2001). Dynamic predictions: oscillations and synchrony in top-down processing. *Nature reviews. Neuroscience*, 2(10), 704–16. doi:10.1038/35094565
- Epstein, R. a, Parker, W. E., & Feiler, A. M. (2007). Where am I now? Distinct roles for parahippocampal and retrosplenial cortices in place recognition. *The Journal of neuroscience : the official journal of the Society for Neuroscience*, 27(23), 6141–9. doi:10.1523/JNEUROSCI.0799-07.2007
- Epstein, R., Harris, A., Stanley, D., & Kanwisher, N. (1999). The Parahippocampal Place Area: Recognition, Navigation, or Encoding? *Significance*, 23, 115–125.
- Ernst, M. O., & Banks, M. S. (2002). Humans integrate visual and haptic information in a statistically optimal fashion. *Nature*, 415(6870), 429–33. doi:10.1038/415429a
- Ernst, M. O., & Bühlhoff, H. H. (2004). Merging the senses into a robust percept. *Trends in cognitive sciences*, 8(4), 162–9. doi:10.1016/j.tics.2004.02.002
- Etienne, A. S., & Jeffery, K. J. (2004). Path Integration in Mammals. *Sciences-New York*, 192, 180 –192. doi:10.1002/hipo.10173
- Etienne, A. S., Maurer, R., Berlie, J., Reverin, B., Rowe, T., Georgakopoulos, J., & Séguinot, V. (1998). Navigation through vector addition. *Nature*, 161–164.
- Etienne, A. S., Maurer, R., & Séguinot, V. (1996). Path integration in mammals and its interaction with visual landmarks. *The Journal of experimental biology*, 199(Pt 1), 201–9.
- Eysel, U. T. (1982). Functional reconnections without new axonal growth in a partially denervated visual relay nucleus. *Nature*, 299(5882), 442–444. doi:10.1038/299442a0
- Fechner, G. T. (1860). *Elemente der Psychophysik*. Leipzig: Breitkopf & Härtel.
- Feldenkrais, M. (2005). *Body and Mature Behavior: A Study of Anxiety, Sex, Gravitation, and Learning*. Frog Books.
- Feldman, D. E., & Brecht, M. (2005). Map plasticity in somatosensory cortex. *Science (New York, N.Y.)*, 310(5749), 810–5. doi:10.1126/science.1115807
- Finelli, L., Baumann, H., Borbély, A., & Achermann, P. (2000). Dual electroencephalogram markers of human sleep homeostasis: correlation between theta activity in waking and slow-wave activity in sleep. *Neuroscience*, 101(3), 523–529. doi:10.1016/S0306-4522(00)00409-7
- Flash, T., & Sejnowski, T. J. (2001). Computational approaches to motor control. *Current opinion in neurobiology*, 11(6), 655–62.
- Fodor, J. (1975). *The language of thought*. New York: Thomas Crowell.
- Fodor, J. (2000). *The Mind Doesn't Work that Way: The Scope and Limits of Computational Psychology*. Cambridge, MA: MIT Press.
- Francis, S. T., Kelly, E. F., Bowtell, R., Dunseath, W. J., Folger, S. E., & McGlone, F. (2000). fMRI of the responses to vibratory stimulation of digit tips. *NeuroImage*, 11(3), 188–202. doi:10.1006/nimg.2000.0541
- Franzius, M., Sprekeler, H., & Wiskott, L. (2007). Slowness and sparseness lead to place, head-direction, and spatial-view cells. *PLoS computational biology*, 3(8), e166. doi:10.1371/journal.pcbi.0030166
- Friston, K. (2010). The free-energy principle: a unified brain theory? *Nature Reviews Neuroscience*, 11(2), 127–38.
- Froese, T. (2010). From Cybernetics to Second-Order Cybernetics : A Comparative Analysis of Their Central Ideas. *Constructivist Foundations*, 5(2), 75–85.
- Froese, T. (2011). From Second-order Cybernetics to Enactive Cognitive Science: Varela's Turn From Epistemology to Phenomenology. *Systems Research and Behavioral Science*, 28(6), 631–645. doi:10.1002/sres.1116
- Froese, T. (2012). From adaptive behavior to human cognition: a review of Enaction. *Adaptive Behavior*, (February). doi:10.1177/1059712311433892
- Froese, T., Gould, C., & Barrett, A. (2011). Re-viewing from Within. A commentary on First- and second-person methods in the science of consciousness. *Constructivist Foundations*, 6(2), 254 – 269.
- Froese, T., McGann, M., Bigge, W., Spiers, A., & Seth, A. K. (2011). The Enactive Torch: A New Tool for the Science of Perception. *IEEE Transactions on Haptics*. doi:10.1109/TOH.2011.57
- Froese, T., & Paolo, Di, E. A. (2011). The enactive approach: Theoretical sketches from cell to society. *Pragmatics & Cognition*, 19(1), 1–36. doi:10.1075/pc.19.1.01fro
- Froese, T., & Stewart, J. (2010). Life After Ashby: Ultrastability and the Autopoietic Foundations of Biological Autonomy. *Cybernetics and Human Knowing*, 17(4), 7–50.
- Froese, T., & Ziemke, T. (2009). Enactive artificial intelligence: Investigating the systemic organization of life and mind. *Artificial Intelligence*, 173(3-4), 466–500. doi:10.1016/j.artint.2008.12.001

- Fujita, N., Klatzky, R. L., Loomis, J. M., & Golledge, R. G. (1993). The Encoding-Error Model of Pathway Completion without Vision. *Geographical Analysis*, 25(4), 295–314.
- Gallagher, S. (2000). Philosophical conceptions of the self: implications for cognitive science. *Trends in cognitive sciences*, 4(1), 14–21.
- Gallagher, S., & Zahavi, D. (2006). *The phenomenological mind: an introduction to philosophy of mind and cognitive science*. London: Routledge.
- Gallant, J. L., Connor, C. E., & Van Essen, D. C. (1998). Neural activity in areas V1, V2 and V4 during free viewing of natural scenes compared to controlled viewing. *Neuroreport*, 9(9), 2153–8.
- Gardiner, J. M. (2001). Episodic memory and autoeotic consciousness: a first-person approach. *Philosophical transactions of the Royal Society of London. Series B, Biological sciences*, 356(1413), 1351–61. doi:10.1098/rstb.2001.0955
- Gardner, H. (1985). *The mind's new science. A History of the Cognitive Revolution*. New York: Basic Books.
- Gassert, R., Yamamoto, A., Chapuis, D., Dovat, L., Bleuler, H., & Burdet, E. (2006). Actuation Methods for Applications in MR Environments. *Concepts in Magnetic Resonance Part B: Magnetic Resonance Engineering*, 29(B)4(1). doi:DOI 10.1002/cmr.b.20070
- Gendlin, E. (1962). *Experiencing and the creation of meaning. A philosophical and psychological approach to the subjective*. New York: Free Press of Glencoe.
- Gendlin, E. (2007). *Focusing*. New York: Books, Bantam.
- Ghazanfar, A. a, & Schroeder, C. E. (2006). Is neocortex essentially multisensory? *Trends in cognitive sciences*, 10(6), 278–85. doi:10.1016/j.tics.2006.04.008
- Gibson, J. J. (1979). *The Ecological Approach to Visual Perception. The Journal of the Society of Architectural Historians* (Vol. 40, p. 332). Houghton Mifflin. doi:10.2307/989638
- Gigerenzer, G., & Todd, P. M. (1999). *Simple heuristics that make us smart*. New York: Oxford University Press.
- Gilbert, S. J., & Walsh, V. (2004). Vision: The Versatile “Visual” Cortex. *Current*, 14, 1056–1057. doi:10.1016/j.cub.2004.11.046
- Ginsburg, C. (2010). *The Intelligence of Moving Bodies: A Somatic View Of Life And Its Consequences*. (Aware. Press, Ed.). SantaFe.
- Glaser, B. G., & Strauss, A. L. (2009). *The discovery of grounded theory: strategies for qualitative research*. Aladin.
- Glenberg, a M. (1997). What memory is for. *The Behavioral and brain sciences*, 20(1), 1–19; discussion 19–55.
- Gramann, K., Gwin, J. T., Bigdely-Shamlo, N., Ferris, D. P., & Makeig, S. (2010). Visual evoked responses during standing and walking. *Frontiers in human neuroscience*, 4(October), 202. doi:10.3389/fnhum.2010.00202
- Graziano, M. S. A. (2006). The organization of behavioral repertoire in motor cortex. *Annual review of neuroscience*, 29, 105–34. doi:10.1146/annurev.neuro.29.051605.112924
- Graziano, M. S. A., Patel, K. T., & Taylor, C. S. R. (2004). Mapping from motor cortex to biceps and triceps altered by elbow angle. *Journal of neurophysiology*, 92(1), 395–407. doi:10.1152/jn.01241.2003
- Green, D. M., & Swets, J. A. (1964). *Signal detection theory and psychophysics*. New York: Wiley.
- Greeno, J. G. (1994). Gibson's Affordances. *Psychological Review*, 101(2), 336–342.
- Gyr, J. W., Brown, J. S., Willey, R., & Zivian, A. (1966). Computer simulation and psychological theories of perception. *Psychological bulletin*, 65(3), 174–92. doi:10.1037/h0022945
- Hafner, V. V., Fend, M., König, P., & Körding, K. P. (2004). Predicting Properties of the Rat Somatosensory System by Sparse Coding. *Neuronal Information Processing*, 4(1), 11–18.
- Hafting, T., Fyhn, M., Molden, S., Moser, M.-B., & Moser, E. I. (2005). Microstructure of a spatial map in the entorhinal cortex. *Nature*, 436(7052), 801–6. doi:10.1038/nature03721
- Hagen, M. C., Franzen, O., McGlone, F., Essick, G., Dancer, C., & Pardo, J. V. (2002). Tactile motion activates the human middle temporal/V5 (MT/V5) complex. *European Journal of Neuroscience*, 16(5), 957–964. doi:10.1046/j.1460-9568.2002.02139.x
- Hamker, F. H. (2006). Modeling feature-based attention as an active top-down inference process. *Bio Systems*, 86(1-3), 91–9. doi:10.1016/j.biosystems.2006.03.010
- Harnard, S. (1990). The symbol grounding problem. *Physica D: Nonlinear Phenomena*, 42(1-3), 335–346. doi:10.1016/0167-2789(90)90087-6
- Harrington, G. S., & Hunter Downs, J. (2001). fMRI mapping of the somatosensory cortex with vibratory stimuli. Is there a dependency on stimulus frequency? *Brain research*, 897(1-2), 188–92.

- Harrington, G. S., Wright, C. T., & Downs, J. H. (2000). A new vibrotactile stimulator for functional MRI. *Human brain mapping, 10*(3), 140–5.
- Hartley, T., Maguire, E. A., Spiers, H. J., & Burgess, N. (2003). The well-worn route and the path less traveled: distinct neural bases of route following and wayfinding in humans. *Neuron, 37*(5), 877–88.
- Harvey, I., Di Paolo, E., Wood, R., Quinn, M., & Tuci, E. (2005). Evolutionary robotics: a new scientific tool for studying cognition. *Artificial life, 11*(1-2), 79–98. doi:10.1162/1064546053278991
- Haugeland, J. (1991). Representational genera. In W. Ramsey, S. Stich, & R. D. (Eds.), *Philosophy and connectionist theory*. New Jersey: Earlbaum.
- Hayhoe, M. M., & Ballard, D. H. (2005). Eye movements in natural behavior. *Trends in cognitive sciences, 9*(4), 188–94. doi:10.1016/j.tics.2005.02.009
- Hayhoe, M. M., & Rothkopf, C. A. (2011). Vision in the natural world. *Wiley Interdisciplinary Reviews: Cognitive Science, 2*(2), 158–166. doi:10.1002/wcs.113
- Hebb, D. O. (1949). *The Organization of Behavior: A Neuropsychological Theory*. New York: Wiley.
- Heed, T., Beurze, S. M., Toni, I., Röder, B., & Medendorp, W. P. (2011). Functional rather than effector-specific organization of human posterior parietal cortex. *The Journal of neuroscience : the official journal of the Society for Neuroscience, 31*(8), 3066–76. doi:10.1523/JNEUROSCI.4370-10.2011
- Hegarty, M., Richardson, A. E., Montello, D. R., Lovelace, K., & Subbiah, I. (2002). Development of a self-report measure of environmental spatial ability. *Intelligence, 30*(5), 425–447. doi:10.1016/S0160-2896(02)00116-2
- Heinen, S. J., & Skavenski, A. A. (1991). Recovery of visual responses in foveal V1 neurons following bilateral foveal lesions in adult monkey. *Experimental Brain Research, 83*(3), 670–674. doi:10.1007/BF00229845
- Held, R. (1965). Plasticity in sensory-motor systems. *Scientific American, 213*(5), 84–94.
- Henderson, J. M., Brockmole, J. R., Castelano, M. S., & Mack, M. (2006). Visual saliency does not account for eye-movements during visual search in real-world scenes. In R. van Gompel, M. Fischer, W. Murray, & R. Hill (Eds.), *Eye movement research: Insights into mind and brain*. Oxford: Elsevier.
- Hendricks, M. (2009). Experiencing Level. *Journal of Consciousness Studies, 16*(10-12), 129–155.
- Hill, D. L. (2004). Neural Plasticity in the Gustatory System. *Nutrition Reviews, 62*(11), S208–S217. doi:10.1111/j.1753-4887.2004.tb00101.x
- Hipp, J., Einhäuser, W., Conrath, J., & König, P. (2005). Learning of somatosensory representations for texture discrimination using a temporal coherence principle. *Network: Computation in Neural Systems, 16*(2-3), 223–238. doi:10.1080/09548980500361582
- Hoffmann, H., Schenck, W., & Möller, R. (2005). Learning visuomotor transformations for gaze-control and grasping. *Biological cybernetics, 93*(2), 119–30. doi:10.1007/s00422-005-0575-x
- Hommel, B., Müsseler, J., Aschersleben, G., & Prinz, W. (2001). The Theory of Event Coding (TEC): a framework for perception and action planning. *The Behavioral and brain sciences, 24*(5), 849–78; discussion 878–937.
- Hornig, S. H., & Sur, M. (2006). Visual activity and cortical rewiring: activity-dependent plasticity of cortical networks. *Progress in brain research, 157*, 3–11. doi:10.1016/S0079-6123(06)57001-3
- Hubel, D. H., & Wiesel, T. N. (1959). Receptive fields of single neurones in the cat's striate cortex. *The Journal of physiology, 148*, 574–91.
- Hunt, G. M. K. (1999). *Philosophy of enquiry*. Coventry.
- Hurlburt, R. T., & Akhter, S. A. (2006). The Descriptive Experience Sampling method. *Phenomenology and the Cognitive Sciences, 5*(3-4), 271–301. doi:10.1007/s11097-006-9024-0
- Hurlburt, R. T., & Heavey, C. L. (2001). Telling what we know: describing inner experience. *Trends in Cognitive Sciences, 5*(9), 400–403.
- Hurley, S. (1998). *Consciousness in action*. London: Harvard University Press.
- Hurley, S. (2006). Varieties of externalism. In R. Menary (Ed.), *The Extended Mind*. Cambridge: MIT Press.
- Husain, M., & Nachev, P. (2007). Space and the parietal cortex. *Trends in cognitive sciences, 11*(1), 30–6. doi:10.1016/j.tics.2006.10.011
- Hutchins, E. (1995). *Cognition in the Wild*. Cambridge, MA: MIT Press.
- Hyvärinen, A., & Hoyer, P. O. (2001). A two-layer sparse coding model learns simple and complex cell receptive fields and topography from natural images. *Vision research, 41*(18), 2413–23.
- Hölzel, B. K., Ott, U., Gard, T., Hempel, H., Weygandt, M., Morgen, K., & Vaitl, D. (2008). Investigation of mindfulness meditation practitioners with voxel-based morphometry. *Social cognitive and affective neuroscience, 3*(1), 55–61. doi:10.1093/scan/nsm038

- Itomi, K., Kakigi, R., Hoshiyama, M., & Watanabe, K. (2001). A unique area of the homonculus: the topography of the primary somatosensory cortex in humans following posterior scalp and shoulder stimulation. *Brain topography*, *14*(1), 15–23.
- Itti, L., & Koch, C. (2001). Computational modelling of visual attention. *Nature reviews. Neuroscience*, *2*(3), 194–203. doi:10.1038/35058500
- Jacobs, J., Kahana, M. J., Ekstrom, A. D., Mollison, M. V, & Fried, I. (2010). A sense of direction in human entorhinal cortex. *Proceedings of the National Academy of Sciences of the United States of America*. doi:10.1073/pnas.0911213107
- James, W. (1890). *The Principles of Psychology* (Vol. 1.). New York: Henry Holt.
- Jenkins, W. M., Merzenich, M. M., Ochs, M. T., Allard, T., & Guic-Robles, E. (1990). Functional reorganization of primary somatosensory cortex in adult owl monkeys after behaviorally controlled tactile stimulation. *Journal of neurophysiology*, *63*(1), 82–104.
- Johnson, G. L. und M. (1980). *Metaphors We Live By*. University of Chicago Press.
- Jones, M. W., & Wilson, M. a. (2005). Theta rhythms coordinate hippocampal-prefrontal interactions in a spatial memory task. *PLoS biology*, *3*(12), e402. doi:10.1371/journal.pbio.0030402
- Just, M. A., Cherkassky, V. L., Aryal, S., & Mitchell, T. M. (2010). A neurosemantic theory of concrete noun representation based on the underlying brain codes. *PloS one*, *5*(1), e8622. doi:10.1371/journal.pone.0008622
- Jäkel, F., & Wichmann, F. A. (2006). Spatial four-alternative forced-choice method is the preferred psychophysical method for naïve observers. *Journal of vision*, *6*(11), 1307–22. doi:10.1167/6.11.13
- Kaas, J. H. (1991). Plasticity of sensory and motor maps in adult mammals. *Annual Review of Neuroscience*.
- Kahane, P., Hoffmann, D., Minotti, L., & Berthoz, A. (2003). Reappraisal of the Human Vestibular Cortex by Cortical Electrical Stimulation Study. *Annals of Neurology*, *54*(5), 615–624. doi:10.1002/ana.10726
- Kahneman, D. (2003). Maps of Bounded Rationality: Psychology for Behavioral Economics. *American Economic Review*, *93*(5), 1449–1475. doi:10.1257/000282803322655392
- Kaida, K., Takahashi, M., Akerstedt, T., Nakata, A., Otsuka, Y., Haratani, T., & Fukasawa, K. (2006). Validation of the Karolinska sleepiness scale against performance and EEG variables. *Clinical neurophysiology : official journal of the International Federation of Clinical Neurophysiology*, *117*(7), 1574–81. doi:10.1016/j.clinph.2006.03.011
- Kaiser, M., Hilgetag, C. C., & Kötter, R. (2010). Hierarchy and dynamics of neural networks. *Frontiers in neuroinformatics*, *4*(August), 10–12. doi:10.3389/fninf.2010.00112
- Kandel, E. R., Schwartz, J. H., & Jessel, T. M. (2000). *Principles of Neural Science*. New York: McGraw-Hill.
- Karnath, H. O. (2001). New insights into the functions of the superior temporal cortex. *Neuroscience*, *2*(August), 568–576.
- Karnath, H. O., & Dieterich, M. (2006). Spatial neglect--a vestibular disorder? *Brain : a journal of neurology*, *129*(Pt 2), 293–305. doi:10.1093/brain/awh698
- Karnath, H. O., Ferber, S., & Himmelbach, M. (2001). Spatial awareness is a function of the temporal not the posterior parietal lobe. *Nature*, *411*(6840), 950–3. doi:10.1038/35082075
- Karnath, H. O., Fruhmann Berger, M., Küker, W., & Rorden, C. (2004). The anatomy of spatial neglect based on voxelwise statistical analysis: a study of 140 patients. *Cerebral cortex (New York, N.Y. : 1991)*, *14*(10), 1164–72. doi:10.1093/cercor/bhh076
- Kayser, C., Körding, K. P., & König, P. (2004). Processing of complex stimuli and natural scenes in the visual cortex. *Current opinion in neurobiology*, *14*(4), 468–73. doi:10.1016/j.conb.2004.06.002
- Keyser, J. (2010). *Preparation of an MR-compatible vibrotactile sensory augmentation device and an fMRI study to assess its effects on path integration*. University of Osnabrück.
- Kilgard, M. P., & Merzenich, M. M. (1998). Cortical Map Reorganization Enabled by Nucleus Basalis Activity. *Science*, *279*(March).
- Kirsh, D. (1996). Adapting the Environment Instead of Oneself. *Adaptive Behavior*, *4*(3-4), 415–452. doi:10.1177/105971239600400307
- Klein, R. (2011). Donald Olding Hebb. *Scholarpedia*, *6*(4), 3719. doi:10.4249/scholarpedia.3719
- Knill, D. C., & Pouget, A. (2004). The Bayesian brain: the role of uncertainty in neural coding and computation. *Trends in neurosciences*, *27*(12), 712–9. doi:10.1016/j.tins.2004.10.007
- Koch, C. (2004). *The Quest for Consciousness: A neurobiological approach*. Roberts & Company Publishers.
- Koch, C., & Ullman, S. (1985). Shifts in selective visual attention: towards the underlying neural circuitry. *Human neurobiology*, *4*(4), 219–27.

- Kohler, I. (1962). Experiments with goggles. *Scientific American*, 206, 62–72.
- Kording, K. P. (2011). Of Toasters and Molecular Ticker Tapes. (K. J. Friston, Ed.) *PLoS Computational Biology*, 7(12), e1002291. doi:10.1371/journal.pcbi.1002291
- Krieger, G., Rentschler, I., Hauske, G., Schill, K., & Zetsche, C. (2000). Object and scene analysis by saccadic eye-movements: an investigation with higher-order statistics. *Spatial vision*, 13(2-3), 201–14.
- Krubitzer, L., & Kaas, J. H. (1989). Striate cortex lesions in monkeys deactivate neurons in the middle temporal visual area (MT). *Invest. Ophthalmol. Vis. Sci.*, 30.
- Kuffler, S. W. (1953). Discharge patterns and functional organization of mammalian retina. *Journal of neurophysiology*, 16(1), 37–68.
- Kupers, R., Fumal, A., De Noordhout, A. M., Gjedde, A., Schoenen, J., & Ptito, M. (2006). Transcranial magnetic stimulation of the visual cortex induces somatotopically organized qualia in blind subjects. *Proceedings of the National Academy of Sciences of the United States of America*, 103(35), 13256–60. doi:10.1073/pnas.0602925103
- Kurthen, M. (1994). *Hermeneutische Kognitionswissenschaft. Die Krise der Orthodoxie*. Bonn: Djre Verlag.
- Kwok, V., Niu, Z., Kay, P., Zhou, K., Mo, L., Jin, Z., So, K.-F., et al. (2011). Learning new color names produces rapid increase in gray matter in the intact adult human cortex. *Proceedings of the National Academy of Sciences*. doi:10.1073/pnas.1103217108
- König, P., & Krüger, N. (2006). Symbols as self-emergent entities in an optimization process of feature extraction and predictions. *Biological cybernetics*, 94(4), 325–34. doi:10.1007/s00422-006-0050-3
- Körding, K. P., Kayser, C., Einhäuser, W., & König, P. (2004). How are complex cell properties adapted to the statistics of natural stimuli? *Journal of neurophysiology*, 91(1), 206–12. doi:10.1152/jn.00149.2003
- Lakatos, I. (1976). *Proofs and Refutations*. Cambridge: Cambridge University Press.
- Land, M. F., & Hayhoe, M. M. (2001). In what ways do eye movements contribute to everyday activities? *Vision Research*, 41, 3559–3565.
- Larkum, M. E., Zhu, J. J., & Sakmann, B. (1999). A new cellular mechanism for coupling inputs arriving at different cortical layers. *Nature*, 398(6725), 338–41. doi:10.1038/18686
- Lazer, D., Pentland, A., Adamic, L., Aral, S., Barabási, A.-L., Brewer, D., Christakis, N., et al. (2009). Social science. Computational social science. *Science (New York, N.Y.)*, 323(5915), 721–3. doi:10.1126/science.1167742
- Lee, D., & Kalmus, H. (1980). The Optic Flow Field: The Foundation of Vision [and Discussion]. *Philosophical Transactions of the Royal Society B: Biological Sciences*, 290(1038), 169–179. doi:10.1098/rstb.1980.0089
- Lee, I., & Kesner, R. P. (2003). Time-dependent relationship between the dorsal hippocampus and the prefrontal cortex in spatial memory. *The Journal of neuroscience : the official journal of the Society for Neuroscience*, 23(4), 1517–23.
- Lenggenhager, B., Smith, S. T., & Blanke, O. (2006). Functional and neural mechanisms of embodiment: importance of the vestibular system and the temporal parietal junction. *Reviews in the neurosciences*, 17(6), 643–57.
- Leopold, D. A., & Logothetis, N. K. (1999). Multistable phenomena: changing views in perception. *Trends in Cognitive Sciences*, 6613(July), 254–264.
- Lettvin, J. Y., Maturana, H. R., McCulloch, W. S. S., & Pitts, W. (1959). What the frog's eye tells the frog's brain. *Proceedings of the IRE*, 47(11), 1940–1951. doi:10.1109/JRPROC.1959.287207
- Levine, J. (1983). Materialism and qualia: the explanatory gap. *Pacific Philosophical Quarterly*, 64, 354–361.
- Lewicki, M. S., & Olshausen, B. A. (1999). Probabilistic framework for the adaptation and comparison of image codes. *Journal of the Optical Society of America A*, 16(7), 1587. doi:10.1364/JOSAA.16.001587
- Livingstone, M., & Hubel, D. (1988). Segregation of form, color, movement, and depth: anatomy, physiology, and perception. *Science (New York, N.Y.)*, 240(4853), 740–9.
- Loomis, J. M., Klatzky, R. L., Golledge, R. G., Cicinelli, J. G., Pellegrino, J. W., & Fry, P. A. (1993). Nonvisual navigation by blind and sighted: Assessment of path integration ability. *Journal of Experimental Psychology General*, 122, 73–73.
- Lungarella, M., & Sporns, O. (2006). Mapping information flow in sensorimotor networks. *PLoS computational biology*, 2(10), e144. doi:10.1371/journal.pcbi.0020144
- Lutz, A., Lachaux, J., Martinerie, J., & Varela, F. J. (2002). Guiding the study of brain dynamics by using first-person data: synchrony patterns correlate with ongoing conscious states during a simple visual

- task. *Proceedings of the National Academy of Sciences of the United States of America*, 99(3), 1586–91. doi:10.1073/pnas.032658199
- Maass, W., Natschläger, T., & Markram, H. (2002). Real-time computing without stable states: a new framework for neural computation based on perturbations. *Neural computation*, 14(11), 2531–60. doi:10.1162/089976602760407955
- Maldjian, J. A., Gottschalk, A., Patel, R. S. S., Pincus, D., Detre, J., & Alsop, D. C. C. (1999). Mapping of secondary somatosensory cortex activation induced by vibrational stimulation: an fMRI study. *Brain research*, 824(2), 291–5.
- Maldjian, J. A., Laurienti, P. J., Kraft, R., & Burdette, J. H. (2003). An automated method for neuroanatomic and cytoarchitectonic atlas-based interrogation of fMRI data sets. *Science*, 19(3), 1233–1239. doi:10.1016/S1053-8119(03)00169-1
- Mannan, S. K., Ruddock, K. H., & Wooding, D. S. (1996). The relationship between the locations of spatial features and those of fixations made during visual examination of briefly presented images. *Spatial vision*, 10(3), 165–88.
- Mannan, S. K., Ruddock, K. H., & Wooding, D. S. (1997). Fixation sequences made during visual examination of briefly presented 2D images. *Spatial vision*, 11(2), 157–78. doi:http://dx.doi.org/10.1163/156856897X00177
- Markram, H. (1997). Regulation of Synaptic Efficacy by Coincidence of Postsynaptic APs and EPSPs. *Science*, 275(5297), 213–215. doi:10.1126/science.275.5297.213
- Marlinski, V., & McCrea, R. A. (2008). Coding of self-motion signals in ventro-posterior thalamus neurons in the alert squirrel monkey. *Experimental Brain Research*, 189(4), 463–472. doi:10.1007/s00221-008-1442-5
- Marr, D. (1976). From understanding computation to understanding neural circuitry. *Neurosci Res Prog Bull*, 15, 470–488.
- Martin, K. A. C. (1994). A brief history of the “feature detector”. *Cerebral cortex (New York, N.Y. : 1991)*, 4(1), 1–7. doi:10.1093/cercor/4.1.1
- Maturana, H. R., & Varela, F. J. (1992). *The Tree of Knowledge: The Biological Roots of Human Understanding. Cognition* (Vol. Rev. ed, p. 269). Shambhala.
- May, A., & Gaser, C. (2006). Magnetic resonance-based morphometry: a window into structural plasticity of the brain. *Current opinion in neurology*, 19(4), 407–11. doi:10.1097/01.wco.0000236622.91495.21
- May, A., Hajak, G., Ganssbauer, S., Steffens, T., Langguth, B., Kleijung, T., & Eichhammer, P. (2007). Structural brain alterations following 5 days of intervention: dynamic aspects of neuroplasticity. *Cerebral cortex (New York, N.Y. : 1991)*, 17(1), 205–10. doi:10.1093/cercor/bhj138
- Mazaika, P. K. (2007). Classifying single trial fMRI : What can machine learning learn ? *Memory*.
- McCulloch, W. S., & Pitts, W. (1943). A logical calculus of the ideas immanent in nervous activity. *The Bulletin of Mathematical Biophysics*, 5(4), 115–133. doi:10.1007/BF02478259
- McGann, M. (2010). Perceptual Modalities: Modes of Presentation or Modes of Interaction? *Journal of Consciousness Studies*, 17.
- McLellan, E., MacQueen, K. M., & Neidig, J. L. (2003). Beyond the Qualitative Interview: Data Preparation and Transcription. *Field Methods*, 15(1), 63–84. doi:10.1177/1525822X02239573
- Medendorp, W. P. (2011). Spatial constancy mechanisms in motor control. *Philosophical transactions of the Royal Society of London. Series B, Biological sciences*, 366(1564), 476–91. doi:10.1098/rstb.2010.0089
- Meier, J. D., Aflalo, T. N., Kastner, S., & Graziano, M. S. A. (2008). Complex organization of human primary motor cortex: a high-resolution fMRI study. *Journal of neurophysiology*, 100(4), 1800–12. doi:10.1152/jn.90531.2008
- Merabet, L. B., Swisher, J. D., McMains, S. A., Halko, M. A., Amedi, A., Pascual-Leone, A., & Somers, D. C. (2007). Combined activation and deactivation of visual cortex during tactile sensory processing. *Journal of neurophysiology*, 97(2), 1633–41. doi:10.1152/jn.00806.2006
- Merleau-Ponty, M. (1962). *Structure of behavior*. Boston: Beacon Press.
- Metzinger, T. (2000). *Neural Correlates of Consciousness: Empirical and Conceptual Questions*. MIT Press.
- Minsky, M. L. (1961). Steps toward artificial intelligence. *Proceedings of the IRE*, 49(1), 8–30.
- Minsky, M. L. (1967). *Computation: Finite and infinite Machines*. Englewood Cliffs, N.j.: Prentice-Hall.
- Mitchell, T. M. (2009). Computer science. Mining our reality. *Science (New York, N.Y.)*, 326(5960), 1644–5. doi:10.1126/science.1174459

- Mitchell, T. M., Shinkareva, S. V., Carlson, A., Chang, K.-M., Malave, V. L., Mason, R. A., & Just, M. A. (2008). Predicting human brain activity associated with the meanings of nouns. *Science (New York, N.Y.)*, 320(5880), 1191–5. doi:10.1126/science.1152876
- Moldonado, P. E., Ossandon, J. P., Flores, F. J., Aboitiz, F., & Cosmelli, D. (2009). Attention and Neurodynamical Correlates of Natural Vision. In F. Aboitiz & D. Cosmelli (Eds.), *From attention to goal directed behavior* (Springer., pp. 63–82). Springer.
- Moore, T., Armstrong, K. M., & Fallah, M. (2003). Visuomotor origins of covert spatial attention. *Neuron*, 40(4), 671–83.
- Morley, I. E., & Hunt, G. M. K. (2000). *Philosophy of Psychology: The Design and Implementation of Theories*. Coventry.
- Müller, K.-R., Tangermann, M., Dornhege, G., Krauledat, M., Curio, G., & Blankertz, B. (2008). Machine learning for real-time single-trial EEG-analysis: from brain-computer interfacing to mental state monitoring. *Journal of neuroscience methods*, 167(1), 82–90. doi:10.1016/j.jneumeth.2007.09.022
- Münzer, S., & Hölscher, C. (2011). Entwicklung und Validierung eines Fragebogens zu räumlichen Strategien. *Diagnostica*, 57(3), 111–125. doi:10.1026/0012-1924/a000040
- Nagel, S. K., Carl, C., Kringe, T., Martin, R., & König, P. (2005). Beyond sensory substitution--learning the sixth sense. *Journal of neural engineering*, 2(4), R13–26. doi:10.1088/1741-2560/2/4/R02
- Nakamura, A., Yamada, T., Goto, A., Kato, T., Ito, K., Abe, Y., Kachi, T., et al. (1998). Somatosensory homunculus as drawn by MEG. *Neuroimage*, 7(4), 377–386. doi:10.1006/nimg.1998.0332
- Navalpakkam, V., & Itti, L. (2007). Search goal tunes visual features optimally. *Neuron*, 53(4), 605–17. doi:10.1016/j.neuron.2007.01.018
- Neisser, U. (1967). *Cognitive Psychology*. New York: Appleton-Century-Crofts.
- Neisser, U. (1976). *Cognition and Reality: Principles and Implications of Cognitive Psychology*. W.H.Freeman & Co Ltd.
- Newell, A. (1973). You can't play 20 questions with nature and win. In W. G. Chase (Ed.), *Visual information processing*. New York: Academic Press.
- Newell, A., & Simon, H. A. (1961). GPS, a program that simulates human thought. In E. Feigenbaum & J. Feldman (Eds.), *Computers and Thought*.
- Newell, A., & Simon, H. A. (1972). *Human Problem Solving*. Englewood Cliffs, N.J.: Prentice-Hall.
- Newell, A., & Simon, H. A. (1976). Computer science as empirical inquiry: symbols and search. *Communications of the ACM*, 19(3), 113–126. doi:10.1145/360018.360022
- Nitz, D. a. (2006). Tracking route progression in the posterior parietal cortex. *Neuron*, 49(5), 747–56. doi:10.1016/j.neuron.2006.01.037
- Norretranders, T. (2002). *Spiere die Welt* (4th ed.). Reinbeck bei Hamburg: Rowohlt.
- Novick, I., & Vaadia, E. (2011). Just Do It: Action-Dependent Learning Allows Sensory Prediction. (T. W. Troyer, Ed.) *PLoS ONE*, 6(10), e26020. doi:10.1371/journal.pone.0026020
- Noë, A. (2002). Is the Visual World a Grand Illusion? *Journal of Consciousness Studies*, (5), 1–12.
- Noë, A. (2004). *Action in Perception*. (H Putnam & N. Block, Eds.) *Perception* (Vol. Representa, p. 277). MIT Press.
- Olshausen, B. A., & Field, D. J. (1996). Emergence of simple-cell receptive field properties by learning a sparse code for natural images. *Nature*, 381(6583), 607–9. doi:10.1038/381607a0
- Olshausen, B. A., & Field, D. J. (1997). Sparse coding with an overcomplete basis set: a strategy employed by V1? *Vision research*, 37(23), 3311–25.
- Olshausen, B. A., & Field, D. J. (2005). How close are we to understanding v1? *Neural computation*, 17(8), 1665–99. doi:10.1162/0899766054026639
- Onat, S., König, P., & Jancke, D. (2011). Natural Scene Evoked Population Dynamics across Cat Primary Visual Cortex Captured with Voltage-Sensitive Dye Imaging. *Cerebral cortex (New York, N.Y. : 1991)*, (November). doi:10.1093/cercor/bhr038
- Oudeyer, P.-Y., Kaplan, F., & Hafner, V. V. (2007). Intrinsic Motivational Systems for Autonomous Mental Developmentkaplan. *IEEE Transactions on Evolutionary Computation*, 11(2), 1–22. doi:10.1109/TEVC.2006.890271
- Overgaard, M., Gallagher, S., & Ramsøy, T. (2008). An integration of first-person methodologies in cognitive science. *Journal of Consciousness*.
- O'Keefe, J., & Burgess, N. (1996). Geometric determinants of the place fields of hippocampal neurons. *Nature*, 381(6581), 425–8. doi:10.1038/381425a0
- O'Regan, J. K., & Noë, A. (2001). A sensorimotor account of vision and visual consciousness. *The Behavioral and brain sciences*, 24(5), 939–73; discussion 973–1031.

- Parkhurst, D. J., Law, K., & Niebur, E. (2002). Modeling the role of salience in the allocation of overt visual attention. *Vision research*, *42*(1), 107–23.
- Parkhurst, D. J., & Niebur, E. (2004). Texture contrast attracts overt visual attention in natural scenes. *The European journal of neuroscience*, *19*(3), 783–9.
- Pascual-Leone, A., Amedi, A., Fregni, F., & Merabet, L. B. (2005). The plastic human brain cortex. *Annual review of neuroscience*, *28*(1), 377–401. doi:10.1146/annurev.neuro.27.070203.144216
- Peters, R. J., Iyer, A., Itti, L., & Koch, C. (2005). Components of bottom-up gaze allocation in natural images. *Vision research*, *45*(18), 2397–416. doi:10.1016/j.visres.2005.03.019
- Petitmengin, C. (2006). Describing one's subjective experience in the second person: An interview method for the science of consciousness. *Phenomenology and the Cognitive Sciences*, *5*(3-4), 229–269. doi:10.1007/s11097-006-9022-2
- Petitmengin, C. (2009). Editorial Introduction. *Journal of Consciousness Studies*, *16*(10-12), 7–19.
- Petitmengin, C., Bitbol, M., Nissou, J., Pachoud, B., Curallucci, H., Cermolacce, M., & Vion-dury, J. (2009). Listening from Within. *Journal of Consciousness Studies*, *16*(10-12), 252–285.
- Pezzulo, G., Barsalou, L. W., Cangelosi, A., Fischer, M. H., McRae, K., & Spivey, M. J. (2011). The Mechanics of Embodiment: A Dialog on Embodiment and Computational Modeling. *Frontiers in Psychology*, *2*(January), 1–21. doi:10.3389/fpsyg.2011.00005
- Pfeifer, R., & Bongard, J. C. (2006). *How The Body Shapes The Way We Think*. Cambridge, MA: MIT Press.
- Pfeifer, R., & Scheier, C. (1999). *Understanding intelligence*. Cambridge, MA: MIT Press.
- Pickering, M. J., & Garrod, S. (2007). Do people use language production to make predictions during comprehension? *Trends in cognitive sciences*, *11*(3), 105–10. doi:10.1016/j.tics.2006.12.002
- Pieper, B., & Clénin, D. (2010). Embodied Perception of Self and Others in Social Action . A Research Perspective Combining Theory and Practice. In F. Boehle & M. Wehrich (Eds.), *Die Körperlichkeit sozialen Handels. Soziale Ordnung jenseits von Normen und Institutionen* (pp. 1–39). Bielefeld: transcript-Verlag.
- Pitts, W., & McCulloch, W. S. (1947). How we know universals; the perception of auditory and visual forms. *The Bulletin of mathematical biophysics*, *9*(3), 127–47. doi:10.1007/BF02478291
- Plihal, W., & Born, J. (1997). Effects of Early and Late Nocturnal Sleep on Declarative and Procedural Memory. *Journal of Cognitive Neuroscience*, *9*(4), 534–547. doi:10.1162/jocn.1997.9.4.534
- Pomplun, M. (2006). Saccadic selectivity in complex visual search displays. *Vision research*, *46*(12), 1886–900. doi:10.1016/j.visres.2005.12.003
- Port, R. F., & Van Gelder, T. (1994). *Mind as Motion. Explorations in the Dynamics of Cognition*. Cambridge, MA: MIT Press.
- Preester, H., & Tsakiris, M. (2009). Body-extension versus body-incorporation: Is there a need for a body-model? *Phenomenology and the Cognitive Sciences*, *8*(3), 307–319. doi:10.1007/s11097-009-9121-y
- Pulvermüller, F., & Fadiga, L. (2010). Active perception: sensorimotor circuits as a cortical basis for language. *Nature reviews. Neuroscience*, *11*(5), 351–60. doi:10.1038/nrn2811
- Putnam, Hilary. (1961). Brains and Behaviour. *American Association for the Advancement of Science*.
- Ramachandran, V. S., Rogers-Ramachandran, D., & Cobb, S. (1995). Touching the phantom limb. *Nature*, *377*(6549), 489–90. doi:10.1038/377489a0
- Rapaport, D., & Stone, J. (1984). The area centralis of the retina in the cat and other mammals: Focal point for function and development of the visual system. *Neuroscience*, *11*(2), 289–301. doi:10.1016/0306-4522(84)90024-1
- Reed, J. L., & Kaas, J. H. (2010). Statistical analysis of large-scale neuronal recording data. *Neural networks : the official journal of the International Neural Network Society*, *23*(6), 673–84. doi:10.1016/j.neunet.2010.04.005
- Reinagel, P., & Zador, A. M. (1999). Natural scene statistics at the centre of gaze. *Network (Bristol, England)*, *10*(4), 341–50.
- Reshef, Finucane, H. K., Grossman, S. R., McVean, G., Turnbaugh, P. J., Lander, E. S., Mitzenmacher, M., et al. (2011). Detecting Novel Associations in Large Data Sets. *Science*, *334*(6062), 1518–1524. doi:10.1126/science.1205438
- Riecke, B. E., Bühlhoff, H. H., & Veen, H. A. H. C. Van. (2002). Visual Homing Is Possible Without Landmarks: A Path Integration Study in Virtual Reality. *Presence: Teleoperators and Virtual Environments*, *11*(5), 443–473. doi:10.1162/105474602320935810
- Riesenhuber, M., & Poggio, T. (1999). Hierarchical models of object recognition in cortex. *Nature neuroscience*, *2*(11), 1019–25. doi:10.1038/14819

- Rizzolatti, G., & Craighero, L. (2010). Premotor theory of attention. *Scholarpedia*, 5(1), 6311. doi:10.4249/scholarpedia.6311
- Rohde, M. (2008). *Evolutionary Robotics Simulation Models in the Study of Human Behaviour and Cognition*. University of Sussex.
- Rothkopf, C. A., Ballard, D. H., & Hayhoe, M. M. (2007). Task and context determine where you look. *Journal of vision*, 7(14), 16.1–20. doi:10.1167/7.14.16
- Roy, D. (2005). Grounding words in perception and action: computational insights. *Trends in cognitive sciences*, 9(8), 389–96. doi:10.1016/j.tics.2005.06.013
- Russel, R. (2004). *Feldenkrais im Überblick: Über den Lernprozeß der Feldenkrais-Methode*. Junfermann.
- Russel, S., & Norvig, P. (2002). *Artificial Intelligence: A Modern Approach* (2nd ed.). Prentice-Hall.
- Russell, N. a, Horii, A., Smith, P. F., Darlington, C. L., & Bilkey, D. K. (2006). Lesions of the vestibular system disrupt hippocampal theta rhythm in the rat. *Journal of neurophysiology*, 96(1), 4–14. doi:10.1152/jn.00953.2005
- Rutishauser, U., & Koch, C. (2007). Probabilistic modeling of eye movement data during conjunction search via feature-based attention. *Journal of vision*, 7(6), 5. doi:10.1167/7.6.5
- Saito, D. N., Okada, T., Honda, M., Yonekura, Y., & Sadato, N. (2006). Practice makes perfect: the neural substrates of tactile discrimination by Mah-Jong experts include the primary visual cortex. *BMC neuroscience*, 7, 79. doi:10.1186/1471-2202-7-79
- Salinas, E., & Sejnowski, T. J. (2001). Book Review: Gain Modulation in the Central Nervous System: Where Behavior, Neurophysiology, and Computation Meet. *The Neuroscientist*, 7(5), 430–440. doi:10.1177/107385840100700512
- Salinas, Emilio, & Abbott, L. F. (2001). Coordinate transformations in the visual system: how to generate gain fields and what to compute with them. In M. A. L. Nicolelis (Ed.), *Advances in Neural Population Coding* (Vol. 130, pp. 175–190). Amsterdam: Elsevier.
- Sanchez-Montanes, M. A., Verschure, P. F. M. J., & König, P. (2000). Local and Global Gating of Synaptic Plasticity. *Neural Computation*, 529, 519–529.
- Save, E., Cressant, A., Thinus-Blanc, C., & Poucet, B. (1998). Spatial firing of hippocampal place cells in blind rats. *The Journal of neuroscience : the official journal of the Society for Neuroscience*, 18(5), 1818–26.
- Schenck, J. F. (2000). Safety of Strong, Static Magnetic Fields. *Journal of Magnetic Resonance Imaging*, 19, 2–19.
- Schneider, E., Villgratner, T., Vockeroth, J., Bartl, K., Kohlbecher, S., Bardins, S., Ulbrich, H., et al. (2009). EyeSeeCam: an eye movement-driven head camera for the examination of natural visual exploration. *Annals of the New York Academy of Sciences*, 1164, 461–7. doi:10.1111/j.1749-6632.2009.03858.x
- Schneider, P., Scherg, M., Dosch, H. G., Specht, H. J., Gutschalk, A., & Rupp, A. (2002). Morphology of Heschl's gyrus reflects enhanced activation in the auditory cortex of musicians. *Nature neuroscience*, 5(7), 688–94. doi:10.1038/nn871
- Schneider, P., Sluming, V., Roberts, N., Scherg, M., Goebel, R., Specht, H. J., Dosch, H. G., et al. (2005). Structural and functional asymmetry of lateral Heschl's gyrus reflects pitch perception preference. *Nature neuroscience*, 8(9), 1241–7. doi:10.1038/nn1530
- Schumann, F. (2004). Embodied cognitive science - is it part of cognitive science? Analysis within a philosophy of science background. *PICS - Publications of the Institute of Cognitive Science*, 3.
- Schumann, F., Einhäuser, W., Vockeroth, J., Bartl, K., Schneider, E., & König, P. (2008). Salient features in gaze-aligned recordings of human visual input during free exploration of natural environments. *Journal of vision*, 8(14), 12.1–17. doi:10.1167/8.14.12
- Schwartz, A. B., Moran, D. W., & Reina, G. A. (2004). Differential representation of perception and action in the frontal cortex. *Science (New York, N.Y.)*, 303(5656), 380–3. doi:10.1126/science.1087788
- Searle, J. (1980). Minds, Brains and Programs. (Jonh Haugeland, Ed.) *Behavioral and Brain Sciences*, 3(3), 417–457.
- Selfridge, O. G. (1958). Pandemonium: a paradigm for learning in mechanisation of thought processes. In D. V. Uttley & B. A. M. (Eds.), *Proceedings of the Symposium on Mechanisation of Thought Processes* (pp. 511–529). London: HMSO.
- Seth, A. K. (2010). Measuring autonomy and emergence via Granger causality. *Artificial life*, 16(2), 179–96. doi:10.1162/artl.2010.16.2.16204

- Shadmehr, R., Smith, M. a, & Krakauer, J. W. (2010). Error correction, sensory prediction, and adaptation in motor control. *Annual review of neuroscience*, 33, 89–108. doi:10.1146/annurev-neuro-060909-153135
- Shannon, C. E. (1948). A Mathematical Theory of Communication. *The Bell System Technical Journal*, 27(July 1928), 379–423.
- Shapley, R., & Lennie, P. (1985). Spatial frequency analysis in the visual system. *Annual review of neuroscience*, 8, 547–83. doi:10.1146/annurev.ne.08.030185.002555
- Sharkey, N., & Ziemke, T. (2001). Mechanistic versus phenomenal embodiment : Can robot embodiment lead to strong AI ? q. *Cognitive Systems Research*, 2, 251–262.
- Shear, J. (1999). *Explaining Consciousness: The Hard Problem*. MIT Press.
- Sheets-Johnstone, M. (1990). *The Roots of Thinking*,. Philadelphia, PA: Temple University Press.
- Shepherd, S. V, Deaner, R. O., & Platt, M. L. (2006). Social status gates social attention in monkeys. *Current biology : CB*, 16(4), R119–20. doi:10.1016/j.cub.2006.02.013
- Shepherd, S. V, & Platt, M. L. (2006). Noninvasive telemetric gaze tracking in freely moving socially housed prosimian primates. *Methods (San Diego, Calif.)*, 38(3), 185–94. doi:10.1016/j.ymeth.2005.12.003
- Shermer, M. (2012). What we don ’ t know. *Nature*, (484), 446–447.
- Siegel, M., Kording, K. P., & König, P. (2000). Integrating top-down and bottom-up sensory processing by somato-dendritic interactions. *Journal of computational neuroscience*, 8(2), 161–73.
- Siegle, J. H., & Warren, W. H. (2010). Distal attribution and distance perception in sensory substitution. *Perception*, 39(2), 208–223. doi:10.1068/p6366
- Simon, H. A. (1972). Theories of Bounded Rationality. In C. B. McGuire & R. Radner (Eds.), *Decision and Organization*. Amsterdam: North-Holland Publishing Company.
- Simoncelli, E. P., & Olshausen, B. A. (2001). Natural image statistics and neural representation. *New York*.
- Smallwood, J., & Schooler, J. W. (2006). The restless mind. *Psychological bulletin*, 132(6), 946–58. doi:10.1037/0033-2909.132.6.946
- Smilek, D., Birmingham, E., Cameron, D., Bischof, W., & Kingstone, A. (2006). Cognitive Ethology and exploring attention in real-world scenes. *Brain research*, 1080(1), 101–19. doi:10.1016/j.brainres.2005.12.090
- Smith, C., & Lapp, L. (1991). Increases in number of REMS and REM density in humans following an intensive learning period. *Sleep*, 14(4), 325–30.
- Smith, E. C., & Lewicki, M. S. (2006). Efficient auditory coding. *Nature*, 439(7079), 978–82. doi:10.1038/nature04485
- Snyder, L. H. (2000). Coordinate transformations for eye and arm movements in the brain. *Current opinion in neurobiology*, 10(6), 747–54.
- Spiers, H. J., & Maguire, E. A. (2004). A “landmark” study on the neural basis of navigation. *Nature Neuroscience*, 7(6), 572–574. doi:10.1038/nn0604-572
- Spiers, H. J., & Maguire, E. A. (2006). Thoughts, behaviour, and brain dynamics during navigation in the real world. *NeuroImage*, 31(4), 1826–40. doi:10.1016/j.neuroimage.2006.01.037
- Sorns, O. (2011). The human connectome: a complex network. *Annals of the New York Academy of Sciences*, 1224(1), 109–25. doi:10.1111/j.1749-6632.2010.05888.x
- Stepankova, K., Pastalkova, E., Kalova, E., Kalina, M., & Bures, J. (2003). A battery of tests for quantitative examination of idiothetic and allothetic place navigation modes in humans. *Behavioural brain research*, 147(1-2), 95–105.
- Stern, D. N. (2002). *The first relationship: Infant and mother. 2002*. Cambridge, MA: Havard University Press.
- Stern, D. N. (2009). Pre-Reflexive Experience and its Passage to Reflexive Experience. A Developmental View. *Journal of Consciousness Studies*, 16(10-12), 307–331.
- Stewart, J., Gapenne, O., & Di Paolo, E. (2011). *Enaction: Towards a New Paradigm for Cognitive Science*. Cambridge, MA: MIT Press.
- Stillings, N. A., Weisler, S. E., Chase, C. H., Feinstein, M. H., Garfield, J. L., & Rissland, E. L. (1995). *Cognitive Science. An introduction*. Cambridge, MA: MIT Press.
- Stuart, G. J., & Sakmann, B. (1994). Active propagation of somatic action potentials into neocortical pyramidal cell dendrites. *Nature*, 367(6458), 69–72.
- Sun, H.-J., Campos, J. L., & Chan, G. S. W. (2004). Multisensory integration in the estimation of relative path length. *Experimental brain research. Experimentelle Hirnforschung. Expérimentation cérébrale*, 154(2), 246–54. doi:10.1007/s00221-003-1652-9

- Sur, M., Garraghty, P., & Roe, A. (1988). Experimentally induced visual projections into auditory thalamus and cortex. *Science*, 242(4884), 1437–1441. doi:10.1126/science.2462279
- Sur, M., & Leamey, C. A. (2001). Development and plasticity of cortical areas and networks. *Neuroscience*, 2(April).
- Synofzik, M., Lindner, A., & Thier, P. (2008). The cerebellum updates predictions about the visual consequences of one's behavior. *Current biology : CB*, 18(11), 814–8. doi:10.1016/j.cub.2008.04.071
- Tatler, B. W. (2007). The central fixation bias in scene viewing : Selecting an optimal viewing position independently of motor biases and image feature distributions. *Journal of Vision*, 7, 1–17. doi:10.1167/7.14.4.Introduction
- Tatler, B. W., Baddeley, R. J., & Vincent, B. T. (2006). The long and the short of it: spatial statistics at fixation vary with saccade amplitude and task. *Vision research*, 46(12), 1857–62. doi:10.1016/j.visres.2005.12.005
- Tatler, B. W., Hayhoe, M. M., Land, M. F., & Ballard, D. H. (2011). Eye guidance in natural vision : Reinterpreting salience. *Journal of Vision*, 11, 1–23. doi:10.1167/11.5.5.Introduction
- Tenenbaum, J. B., Kemp, C., Griffiths, T. L., & Goodman, N. D. (2011). How to Grow a Mind: Statistics, Structure, and Abstraction. *Science*, 331(6022), 1279–1285. doi:10.1126/science.1192788
- Thelen, E., & Smith, L. B. (1994). *A Dynamic Systems approach to the Development of Cognition and Action*. Cambridge, MA: MIT Press.
- Thompson, E. (1997). Symbol Grounding: A Bridge from Artificial Life to Artificial Intelligence. *Brain and Cognition*, 34(1), 48–71.
- Thompson, E. (2004). Life and mind: From autopoiesis to neurophenomenology. A tribute to Francisco Varela 1. *Phenomenology and the Cognitive Sciences*, 381–398.
- Thompson, E. (2005). Sensorimotor subjectivity and the enactive approach to experience. *Phenomenology and the Cognitive Sciences*, 4(4), 407–427. doi:10.1007/s11097-005-9003-x
- Thompson, E. (2007). *Mind in Life: Biology, Phenomenology, and the Sciences of Mind*. Harvard University Press.
- Thompson, E., & Stapleton, M. (2008). Making Sense of Sense-Making: Reflections on Enactive and Extended Mind Theories. *Topoi*, 28(1), 23–30. doi:10.1007/s11245-008-9043-2
- Thompson, E., & Varela, F. J. (2001). Radical embodiment: neural dynamics and consciousness. *Trends in cognitive sciences*, 5(10), 418–425.
- Torralba, A., & Oliva, A. (2003). Statistics of natural image categories. *Network (Bristol, England)*, 14(3), 391–412.
- Torralba, A., Oliva, A., Castelhano, M. S., & Henderson, J. M. (2006). Contextual guidance of eye movements and attention in real-world scenes: the role of global features in object search. *Psychological review*, 113(4), 766–86. doi:10.1037/0033-295X.113.4.766
- Treisman, A. M. (1964). Selective Attention in Man. *British medical bulletin*, 20, 12–6.
- Treisman, A. M. (2003). Consciousness and Perceptual Binding. In A. Cleeremans (Ed.), *The Unity of Consciousness: Binding, Integration and Dissociation*. Oxford: Oxford University Press.
- Treisman, A. M., & Gelade, G. (1980). A feature-integration theory of attention. *Cognitive psychology*, 12(1), 97–136. doi:7351125
- Treue, S. (2001). Neural correlates of attention in primate visual cortex. *Trends in neurosciences*, 24(5), 295–300.
- Treue, S. (2003). Visual attention: the where, what, how and why of saliency. *Current Opinion in Neurobiology*, 13(4), 428–432. doi:10.1016/S0959-4388(03)00105-3
- Trotter, Y., & Celebrini, S. (1999). Gaze direction controls response gain in primary visual-cortex neurons. *Nature*, 398(6724), 239–42. doi:10.1038/18444
- Tsakiris, M., Costantini, M., & Haggard, P. (2008). The role of the right temporo-parietal junction in maintaining a coherent sense of one's body. *Neuropsychologia*, 46(12), 3014–8. doi:10.1016/j.neuropsychologia.2008.06.004
- Tse, Z. T. H., Janssen, H., Hamed, A., Ristic, M., Young, I., & Lamperth, M. (2009). Magnetic resonance elastography hardware design: a survey. *Proceedings of the Institution of Mechanical Engineers. Part H, Journal of engineering in medicine*, 223(4), 497–514.
- Turing, A. M. (1938). On Computable Numbers, with an Application to the Entscheidungsproblem. A Correction. *Proceedings of the London Mathematical Society*, s2-43(6), 544–546. doi:10.1112/plms/s2-43.6.544

- Van Hateren, J. H., & Van der Schaaf, A. (1998). Independent component filters of natural images compared with simple cells in primary visual cortex. *Proceedings. Biological sciences / The Royal Society*, 265(1394), 359–66. doi:10.1098/rspb.1998.0303
- Vann, S. D., & Aggleton, J. P. (2004). Testing the importance of the retrosplenial guidance system: effects of different sized retrosplenial cortex lesions on heading direction and spatial working memory. *Behavioural brain research*, 155(1), 97–108. doi:10.1016/j.bbr.2004.04.005
- Varela, F. J. (1979). *Principles of biological autonomy*. New York: Elsevier North Holland.
- Varela, F. J. (1996). Neurophenomenology: A Methodological Remedy for the Hard Problem. *Journal of Consciousness Studies*, (4), 330–349.
- Varela, F. J., & Shear, J. (1999). First-person Methodologies: What, Why, How? *Journal of Consciousness Studies*, (2), 1–14.
- Varela, F. J., Thompson, E., & Rosch, E. (1991). *The embodied mind: Cognitive science and human experience*. Cambridge, MA: MIT Press.
- Vermersch, P. (2009). Describing the Practice of Introspection. *Journal of Consciousness Studies*, 16(10-12), 20–57.
- Vinje, W. E., & Gallant, J. L. (2000). Sparse Coding and Decorrelation in Primary Visual Cortex During Natural Vision. *Science*, 287(5456), 1273–1276. doi:10.1126/science.287.5456.1273
- Von Melchner, L., Pallas, S. L., & Sur, M. (2000). Visual behaviour mediated by retinal projections directed to the auditory pathway. *Nature*, 404(6780), 871–6. doi:10.1038/35009102
- Vyazovskiy, V., Borbély, A., & Tobler, I. (2000). Fast track: Unilateral vibrissae stimulation during waking induces interhemispheric EEG asymmetry during subsequent sleep in the rat. *Journal of Sleep Research*, 9(4), 367–371. doi:10.1046/j.1365-2869.2000.00230.x
- Wason, P. C. (1966). Reasoning. In B. M. Foss (Ed.), *New horizons in psychology*. Harmondsworth: Penguin.
- Weiller, D., Laer, L., Engel, A. K., & Konig, P. (2010). Unsupervised learning of reflexive and action-based affordances to model adaptive navigational behavior. *Frontiers in neurorobotics*, 4, 2. doi:10.3389/fnbot.2010.00002
- Weiller, D., Martin, R., Dahne, S., Engel, A. K., & Konig, P. (2010). Involving motor capabilities in the formation of sensory space representations. *PLoS one*, 5(4), e10377. doi:10.1371/journal.pone.0010377
- Wheeler, M. A., Stuss, D. T., & Tulving, E. (1997). Toward a theory of episodic memory: the frontal lobes and autothetic consciousness. *Psychological bulletin*, 121(3), 331–54.
- Whishaw, I. Q., & Brooks, B. L. (1999). Calibrating space: exploration is important for allothetic and idiothetic navigation. *Hippocampus*, 9(6), 659–67. doi:10.1002/(SICI)1098-1063(1999)9:6<659::AID-HIPO7>3.0.CO;2-E
- Wichmann, F. A., & Hill, N. J. (2001a). The psychometric function: I. Fitting, sampling, and goodness of fit. *Perception and Psychophysics*, 63(8), 1293–1313.
- Wichmann, F. A., & Hill, N. J. (2001b). The psychometric function: II. Bootstrap-based confidence intervals and sampling. *Perception*, 63(8), 1314–1329.
- Wickens, T. D. (2002). *Elementary Signal Detection Theory*. New York: Oxford University Press.
- Wiener, Jan M, Berthoz, A., & Wolbers, T. (2011). Dissociable cognitive mechanisms underlying human path integration. *Experimental brain research. Experimentelle Hirnforschung. Experimentation cerebrale*, 208(1), 61–71. doi:10.1007/s00221-010-2460-7
- Willems, R. M. (2011). Re-appreciating the why of cognition: 35 years after marr and poggio. *Frontiers in psychology*, 2(September), 244. doi:10.3389/fpsyg.2011.00244
- Wilming, N., Betz, T., Kietzmann, T. C., & Ko, P. (2011). Measures and Limits of Models of Fixation Selection, 6(9). doi:10.1371/Citation
- Wilson, M., & Knoblich, G. (2005). The case for motor involvement in perceiving conspecifics. *Psychological bulletin*, 131(3), 460–73. doi:10.1037/0033-2909.131.3.460
- Wilson, & Mainen, Z. F. (2006). Early events in olfactory processing. *Annual review of neuroscience*, 29, 163–201. doi:10.1146/annurev.neuro.29.051605.112950
- Winograd, T., & Flores, F. (1986). *Understanding Computers and Cognition: A New Foundation for Design*. Norwood, N.J.: Ablex Publishing Corporation.
- Wolbers, T., & Buchel, C. (2005). Dissociable retrosplenial and hippocampal contributions to successful formation of survey representations. *The Journal of neuroscience : the official journal of the Society for Neuroscience*, 25(13), 3333–40. doi:10.1523/JNEUROSCI.4705-04.2005

- Wolbers, T., Weiller, C., & Büchel, C. (2004). Neural foundations of emerging route knowledge in complex spatial environments. *Brain research. Cognitive brain research*, *21*(3), 401–11. doi:10.1016/j.cogbrainres.2004.06.013
- Wolbers, T., Wiener, J. M., Mallot, H. A., & Büchel, C. (2007). Differential recruitment of the hippocampus, medial prefrontal cortex, and the human motion complex during path integration in humans. *The Journal of neuroscience : the official journal of the Society for Neuroscience*, *27*(35), 9408–16. doi:10.1523/JNEUROSCI.2146-07.2007
- Wyss, R., König, P., & Verschure, P. F. M. J. (2006). A model of the ventral visual system based on temporal stability and local memory. *PLoS biology*, *4*(5), e120. doi:10.1371/journal.pbio.0040120
- Yarbus, A. L. (1967). Eye movements and vision. (L. A. Riggs, Ed.) *Problems of Information Transmission*, *160*(3828), 222. doi:10.1126/science.160.3828.657
- Yen, S.-C., Baker, J., & Gray, C. M. (2007). Heterogeneity in the responses of adjacent neurons to natural stimuli in cat striate cortex. *Journal of neurophysiology*, *97*(2), 1326–41. doi:10.1152/jn.00747.2006
- Zhou, C., Zemanová, L., Zamora, G., Hilgetag, C., & Kurths, J. (2006). Hierarchical Organization Unveiled by Functional Connectivity in Complex Brain Networks. *Physical Review Letters*, *97*(23), 3–6. doi:10.1103/PhysRevLett.97.238103