

Edited by Paul Gilbert

# Compassion

Concepts, Research and Applications



ROUTLEDGE



---

# Compassion|

---

Paul Gilbert brings together an international line-up of leading scholars and researchers in the field to provide a state-of-the-art exploration of key areas in compassion research and applications. Compassion can be seen as a core element of prosocial behaviour, and explorations of the concepts and value of compassion have been extended into different aspects of life including physical and psychological therapies, schools, leadership and business.

While many animals share abilities to be distress sensitive and caring of others, it is our newly evolved, socially intelligent abilities that make us capable of *knowingly and deliberately* helping others and purposely developing skills and wisdom to do so. This book generates many research questions whilst exploring the similarities and differences of human compassion to non-human caring and looks at how compassion changes the brain and body, affects genetic expression, manifests at a young age and is then cultivated (or not) by the social environment.

*Compassion: Concepts, Research and Applications* will be essential reading for professionals, researchers and scholars interested in compassion and its applications in psychology and psychotherapy.

**Paul Gilbert**, OBE, is Professor of Clinical Psychology, University of Derby, and has been actively involved in research and treating people with shame-based and mood disorders for over 30 years. He is a past President of the British Association for Cognitive and Behavioural Psychotherapy and a fellow of the British Psychological Society. He was awarded the OBE for contributions to mental health in 2011.

‘This exciting collection of chapters will bring readers up-to-date with the latest developments in compassion research. Compassion has become an essential psychological concept with developmental, biological, and social roots as well as a wide variety of applications.’

**Chris R. Brewin**, Professor of Clinical Psychology, University College London.

‘Given the explosion of interest in compassion in many disciplines and professions, this overview of compassion is extremely timely. Paul Gilbert has assembled a stellar lineup of international experts, and the resulting book is essential for all who are interested in better understanding or fostering compassion. The book is remarkably comprehensive, addressing fundamental definitional and conceptual issues, the psychobiology of compassion, its origin in and impact on relationships, and its potential transformative role in leadership, health care, and psychotherapy. The book brilliantly summarizes the current state of compassion research and application and will serve as a catalyst for future explorations and developments.’

**David C. Zuroff**, Professor of Clinical Psychology, McGill University, Montreal.

‘This remarkable and powerful book links the practice of mindful compassion to basic science and theory effortlessly. Paul Gilbert has assembled and organized a truly excellent anthology of the essential elements regarding Compassion Focused Therapy and the applied research on compassion. Practitioners of evidence-based psychotherapy who wish to remain at the cutting edge of their science need this book. I give this my highest recommendation.’

**Denis Tirsch**, Founding Director, The Center for Compassion Focused Therapy, USA.

First published 2017

by Routledge

2 Park Square, Milton Park, Abingdon, Oxon OX14 4RN

and by Routledge

711 Third Avenue, New York, NY 10017

*Routledge is an imprint of the Taylor & Francis Group, an informa business*

© 2017 selection and editorial matter, Paul Gilbert; individual chapters, the contributors

The right of the editor to be identified as the author of the editorial material, and of the authors for their individual chapters, has been asserted in accordance with sections 77 and 78 of the Copyright, Designs and Patents Act 1988.

All rights reserved. No part of this book may be reprinted or reproduced or utilised in any form or by any electronic, mechanical, or other means, now known or hereafter invented, including photocopying and recording, or in any information storage or retrieval system, without permission in writing from the publishers.

*Trademark notice:* Product or corporate names may be trademarks or registered trademarks, and are used only for identification and explanation without intent to infringe.

*British Library Cataloguing in Publication Data*

A catalogue record for this book is available from the British Library

*Library of Congress Cataloging in Publication Data*

A catalog record for this book has been requested

ISBN: 978-1-138-95718-3 (hbk)

ISBN: 978-1-138-95719-0 (pbk)

ISBN: 978-1-315-56429-6 (ebk)

Typeset in Times New Roman

by Swales & Willis Ltd, Exeter, Devon, UK

---

# Contents|

---

[List of illustrations](#)

[List of contributors](#)

[Preface](#)

## **PART I**

### **Evolution and the nature of compassion**

[1 Compassion: definitions and controversies](#)

PAUL GILBERT

[2 Prehistoric origins: the compassion of far distant strangers](#)

PENNY SPIKINS

[3 Compassion as a social mentality: an evolutionary approach](#)

PAUL GILBERT

[4 Mindfulness and compassion: similarities and differences](#)

CHRISTOPHER GERMER AND THORSTEN BARNHOFER

## **PART II**

### **Compassion and its physiologies**

[5 The body of compassion](#)

JENNIFER S. MASCARO AND CHARLES L. RAISON

[6 The psychobiological foundation of prosocial relationships: the role of oxytocin in daily social exchanges](#)

VALENTINA COLONNELLO, NICOLA PETROCCHI AND MARKUS HEINRICHS

p.vi

[7 Compassion in the autonomic nervous system: the role of the vagus nerve](#)

JENNIFER E. STELLAR AND DACHER KELTNER

[8 Compassion and the brain](#)

PASCAL VRTIČKA, PAULINE FAVRE AND TANIA SINGER

## [9 Behavior genetics of prosocial behavior](#)

CHRISTOPHER C. CONWAY AND GEORGE M. SLAVICH

### **PART III**

#### **Compassion and relationships**

##### [10 Evolution, child raising, and compassionate morality](#)

DARCIA NARVAEZ

##### [11 An attachment perspective on compassion and altruism](#)

MARIO MIKULINCER AND PHILIP R. SHAVER

##### [12 Broaden-and-build theory meets interpersonal neurobiology as a lens on compassion and positivity resonance](#)

BARBARA L. FREDRICKSON AND DANIEL J. SIEGEL

### **PART IV**

#### **Applying compassion**

##### [13 Positive leadership, power and compassion](#)

DANIEL MARTIN AND YOTAM HEINEBERG

##### [14 Compassionate leadership for compassionate health care](#)

MICHAEL A. WEST AND RACHNA CHOWLA

##### [15 The emergence of the compassion focused therapies](#)

JAMES N. KIRBY AND PAUL GILBERT

#### [Index](#)

---

# Illustrations

---

## **Figures**

- [2.1 KNM-ER 1808 showing abnormal layer of bone on the femur](#)
- [2.2 The ‘toothless’ Dmanisi hominin](#)
- [2.3 Olduvai handaxe, Lower Palaeolithic, about 1.2 million years old, Olduvai Gorge, Tanzania](#)
- [3.1 The interactive flow of compassion](#)
- [3.2 Relation of the compassionate self to the flows of compassions](#)
- [3.3 The motivation and competencies of compassion](#)
- [7.1 Vagus nerve innervation](#)
- [8.1 Two different routes for the understanding of others](#)
- [8.2 Two different responses to the suffering of others](#)
- [8.3 Evidence for differential functional brain plasticity after empathy and compassion training](#)
- [14.1 The elements of a compassionate response](#)
- [15.1 Representation of the integrated and therapeutic effects of building the compassionate mind](#)

## **Tables**

- [3.1 A brief guide to social mentalities](#)
- [9.1 Key behaviour genetic findings in research on prosocial behaviour](#)
- [10.1 The effects of the evolved development niche on child outcomes](#)
- [14.1 The essence of effective health care leadership](#)
- [15.1 Evolution informed psychotherapy in CFT](#)
- [15.2 Common and specific features of compassion-based trainings and therapy](#)
- [15.3 The 12 competencies of compassion in CFT](#)

---

## Contributors

---

Thorsten Barnhofer, PhD  
Sir Henry Wellcome Mood Disorders Centre,  
University of Exeter, United Kingdom

Rachna Chowla, PhD  
Albion Street Group Practice, London, United Kingdom;  
EIR INSEAD HMI, Fontainebleau, France

Valentina Colonnello, PhD  
Department of Experimental, Diagnostic and Specialty Medicine,  
University of Bologna, Italy

Christopher C. Conway, PhD  
Department of Psychology, College of William and Mary  
Integrated Science Center, Williamsburg, Virginia, United States

Pauline Favre, PhD, Department of Social Neuroscience,  
Max Planck Institute for Human Cognitive and Brain Sciences,  
Leipzig, Germany

Barbara L. Fredrickson, PhD  
Kenan Distinguished Professor, Director, Social Psychology Doctoral Program,  
Department of Psychology,  
University of North Carolina, United States

Christopher Germer, PhD  
Lecturer on Psychiatry,  
Harvard Medical School, United States

p.ix

Paul Gilbert, PhD OBE  
Centre for Compassion Research and Training,  
College of Health and Social Care Research Centre, University of Derby, United Kingdom

Yotam Heineberg, PhD  
Palo Alto University/Stanford University Center for Compassion and Altruism, Research and Education (CCARE),  
Stanford, United States

Markus Heinrichs, PhD  
Department of Psychology, Laboratory for Biological and Personality Psychology, University of Freiburg, Germany;  
Freiburg Brain Imaging Center, University Medical Center, University of Freiburg, Germany

Dacher Keltner, PhD  
Department of Psychology,  
University of California, Berkeley, United States

James N. Kirby, PhD,  
Lecturer and Clinical Psychologist, School of Psychology,  
University of Queensland, Australia

Daniel Martin, PhD  
California State University, East Bay-Department of Management/Stanford  
University Center for Compassion and Altruism Research and Education (CCARE), Stanford, California, United States

Jennifer S. Mascaró, PhD,  
Department of Family and Preventive Medicine  
Emory University School of Medicine, Atlanta, Georgia

Mario Mikulincer  
School of Psychology  
Interdisciplinary Center (IDC) Herzliya, Israel

Darcia Narvaez, PhD  
Professor of Psychology,  
University of Notre Dame, Indiana, United States

Nicola Petrocchi, PhD  
Department of Economics and Social Sciences, John Cabot University, Rome, Italy;  
Compassionate Mind Italy Association, Rome, Italy



Charles L. Raison, MD,  
Mary Sue and Mike Shannon Chair for Healthy Minds, Children and Families; Professor at the School of Human Ecology;  
Professor, Department of Psychiatry,  
School of Medicine and Public Health, University of Wisconsin-Madison, United States

Phillip R. Shaver, PhD  
Department of Psychology,  
University of California, United States

Daniel J. Siegel, PhD  
Mindsight Institute,  
Santa Monica, California, United States

Tania Singer, PhD  
Director, Department of Social Neuroscience,  
Max Planck Institute for Human Cognitive and Brain Sciences, Leipzig, Germany

George M. Slavich, PhD  
Associate Professor of Psychiatry and Biobehavioral Sciences;  
Research Scientist, Cousins Center for Psychoneuroimmunology;  
Director, Laboratory for Stress Assessment and Research, Cousins Center for Psychoneuroimmunology and Department of Psychiatry and Biobehavioral Sciences,  
University of California, United States

Penny Spikins, PhD  
Department of Archaeology,  
University of York, United Kingdom

Jennifer E. Stellar, PhD  
Assistant Professor,  
University of Toronto, Canada

Dr Pascal Vrtička, PhD  
Group Leader, Department of Social Neuroscience,  
Max Planck Institute for Human Cognitive and Brain Sciences, Leipzig, Germany

Michael A. West, PhD  
Senior Fellow, The King's Fund, London;  
Lancaster University Management School,  
Lancaster, United Kingdom

---

## Preface

---

The last 20 years have seen some outstanding developments in research on prosocial behaviour, ranging over altruism, morality, caring and compassion. Studies have proliferated on how the brain and body respond to both receiving compassion and expressing compassion to self and others. These advances, along with evolutionary understanding, have helped us recognise how fundamentally so much of what we are as humans, even our genetic expressions, is influenced by the quality of care, affiliation and general friendliness there is in our social relationships. From the day we are born to the day we die the helpfulness, kindness and compassion of others will have a huge impact on the quality of our lives.

As with all vibrant areas of research, compassion research is not without its controversies. On the positive side controversies on definition, nature and function show that compassion is a fascinating area that is vigorous, vibrant and open to debate. On the negative side there can be a tendency to try to contain, restrain and limit definitions by adopting certain ones prematurely. In this edited book I have advised authors of my particular view about compassion but have not insisted that they adopt it. So you will find different definitions of compassion in different chapters. Often these reflect the particular focus or research interest of the author(s), which tend to vary.

For me though it has been a privilege to bring together some of the top thinkers and researchers in the field of prosocial behaviour and compassion to explore the array of different areas compassion research is now reaching. From understanding genetic expression, the choreography and architecture of our brains, through to our social relationships and psychotherapy, compassion is beginning to texture how we think about all of these topics. The book is divided into four parts exploring these different and exciting areas.

[Part I](#) considers the evolution and the nature of compassion with my opening piece on definitional issues and controversies. [Chapter 2](#) by Penny Spikins offers fascinating reviews of the archaeological evidence for the gradual development of compassion in early human groups. She makes the point that prosocial, not anti-social, behaviour has been a driver of social intelligence. In (a rather extended) [Chapter 3](#) I spell out a social mentalities approach to compassion. The argument here is that compassion can be understood as caring motivation textured by recently-evolved social intelligent competencies. One of these social intelligent competencies is self-awareness and capacities for intentional mindfulness which is explored in [Chapter 4](#). Here Chris Germer and Thorsten Barnhorfer offer their extensive experience to explore the interactions between mindfulness and compassion.

p.xii

[Part II](#) on the physiologies of compassion begins with [Chapter 5](#) offering an overview of the field from Jennifer Mascaro and Charles Raison, highlighting the importance of many interacting sub-systems in compassion. [Chapter 6](#) by Valentina Colonnello, Nicola Petrocchi and Markus Heinrichs illuminates particular neurophysiological systems, particularly the role of

oxytocin, in compassion and prosocial behaviour in general. [Chapter 7](#) by Jennifer Stellar and Dacher Keltner looks at a different aspect of the parasympathetic system and the vagus nerve associated with compassion. [Chapter 8](#) by Pascal Vrtička, Pauline Favre and Tania Singer moves us into the brain with a review of how compassion and empathy are represented in the brain. This part is rounded off with [Chapter 9](#) by Christopher Conway and George Slavich looking at the fast-developing field of epigenetics and prosocial compassionate behaviour, and in particular the importance of understanding socially guided methylation.

[Part III](#) takes us into the arena of social contexts. In [Chapter 10](#) Darcia Narvaez highlights the importance of social context and early background for the development of a range of prosocial compassionate and moral behaviours. [Chapter 11](#) by Mario Mikulincer and Philip Shaver provides a detailed overview of how early background experiences, particularly of attachment, impact subsequent compassionate and altruistic orientations. [Chapter 12](#) by Barbara Fredrickson and Daniel Siegel provides a unique conversational chapter exploring the interactions between their different backgrounds in micro-moment and micro-interactional patterns with interpersonal neurobiology.

[Part IV](#) explores the importance and difficulties of applying compassion in the real world. [Chapter 13](#) by Daniel Martin and Yotam Heineberg covers a wide-ranging literature on the conflict between prosocial and more antisocial types of leadership, and the challenges for compassion and leadership in organisations. [Chapter 14](#) by Michael West and Rachna Chowla considers the importance of compassionate leadership in healthcare settings like the NHS. They explore some of the management styles that can facilitate or block compassion. Finally, [Chapter 15](#) by James Kirby and myself explores the application of compassion focused approaches to mental health problems and psychotherapy. Our main theme is that as we learn more about the evolved role of affiliative emotions and motives on a range of physiological, psychological social processes, it makes sense that they should become centre ground to therapy.

I hope you find things in this book which will be useful to you and maybe even inspire you. The idea of developing a science for creating a more compassionate prosocial world is exciting and it's also exciting to see so many individuals making this the centre of their research.

## Chapter 6

# The psychobiological foundation of prosocial relationships

## The role of oxytocin in daily social exchanges

*Valentina Colonnello, Nicola Petrocchi and Markus Heinrichs*

---

### **Introduction**

Caring and affiliative motivations are embedded in human nature and rooted in evolutionarily developed brain systems that we share with other mammals (MacLean, 1985; Panksepp & Biven, 2012). They are considered to be the root of compassion (Gilbert, 2009). Compassion can be considered the expression of the extended caregiving system, which is thought to have emerged from evolutionarily ancient motivations to detect and respond to the need of dependent offspring (Gilbert, [Chapters 1](#) and [3](#)). The caring motivation would extend, through evolution, to the welfare of all living beings and the formation of cooperative relations with non-kin (Goetz, Keltner, & Simon-Thomas, 2010; Wang, 2005).

As discussed by Gilbert in [Chapter 1](#), despite growing interest in the subject of compassion, there is little consensus regarding the definition of the notion of compassion itself and its underlying psychobiological mechanisms. Compassion has been conceptualized as both an *affective state*, defined by a specific subjective feeling that arises while witnessing another's suffering (Goetz, Keltner, & Simon-Thomas, 2010), and a motivational state rooted in the evolution of caring emotional system and aimed at the prevention and relief of suffering and its causes. In the latter view, compassion encompasses a variety of characteristics and can give rise to a blend of emotions (Gilbert, 2015). Notably, in Gilbert's view, compassion is a motivational system, a social mentality that influences attention mechanisms towards the social world (Gilbert, [Chapter 3](#), this volume). Thus, compassion relies on several emotions and it is not reducible to a single specific emotion.

Among the psychobiological systems involved in social bond formation and caring, the neuropeptide oxytocin plays a central role (Colonnello, Petrocchi, Farinelli, & Ottaviani, 2016; Donaldson & Young, 2008; Meyer-Lindenberg, Domes, Kirsch, & Heinrichs, 2011; Petrocchi & Couyoumdjian, 2015 for a review). Oxytocin is synthesized in the paraventricular and supraoptic nuclei of the hypothalamus and, through axonal projection, is processed to the posterior pituitary lobes and released for peripheral circulation (Meyer-Lindenberg et al., 2011, for a review). Oxytocin plays a key role in the expression of the caregiving motivation thanks to its receptors in several subcortical areas such as the anterior cingulate and the bed nucleus of the striaterminalis involved in parental behavior (Panksepp, 1998). In addition, the oxytocinergic system is very likely involved in approach/appetitive motivation thanks to its ability to facilitate interactions with the mesolimbic reward-seeking system (Shahrokh, Zhang,

Diorio, Gratton, & Meaney, 2010) and its involvement with vagal dorsal motor nucleus regulation (Carter, 2014; Porges, 2003).

p.106

As several human studies indicate, the oxytocinergic system is involved in several aspects of social interactions as, for example, social bond formation (Galbally, Lewis, IJzendoorn, & Permezel, 2011) conflict resolution (Ditzen et al., 2009), understanding of others' feelings (Schulze et al., 2011), and self-related and other-related processing (Colonnello, Chen, Panksepp, & Heinrichs, 2013; Colonnello, Domes, & Heinrichs, 2016; Colonnello & Heinrichs, 2014). Given the key role of oxytocin in several aspects of positive social behavior, there is increased interest in studying this system's potential involvement in compassion motivation and compassion-related feelings and behaviors.

Compassionate behaviors rely on the understanding of other's emotions while maintaining self/other distinction and regulating personal distress – all aspects found to be modulated by oxytocin. Thus, we will focus on the effects of oxytocin administration on these central components for experiencing compassion, and will consider the possible mediating role of individual traits on oxytocin reception. Throughout this contribution to the field, we will highlight potential links and implications of oxytocin studies with regards to compassion.

## **Oxytocin involvement in caring behavior and distress regulation**

Several studies have demonstrated that the oxytocinergic system plays a key role in the activation of caregiving approach motivation (Meyer-Lindenberg et al., 2011, for a review). For example, Feldman and colleagues (2007) reported that high peripheral oxytocin levels during pregnancy and the early postpartum period are positively associated with gazing at, affectionately touching and checking the infant, typical initial manifestations of maternal care (Feldman, Weller, Zagoory-Sharon, & Levine, 2007). Furthermore, mother–infant behavioral synchrony has been found to correlate positively with maternal salivary and plasma oxytocin levels (Feldman, Gordon, Schneiderman, Weisman, & Zagoory-Sharon, 2010; Feldman, Gordon, & Zagoory-Sharon, 2011).

Independent studies investigating the causal relationship between central oxytocin levels and caregiving behavior reveal that enhanced central levels of oxytocin increase sensitive parenting behaviors. In men, oxytocin administration increases respiratory sinus arrhythmia (an index of parasympathetic activity and readiness to willingly engage in social activity) along with affectionate touch and episodes of social reciprocity during interactions with their infants (Weisman, Zagoory-Sharon, & Feldman, 2012). In addition, the increase in central oxytocin levels promotes feelings of acceptance and other-oriented behaviors: men who received oxytocin revealed less hostile behavior than placebo-treated fathers during play sessions with their toddlers (Naber, van IJzendoorn, Deschamps, van Engeland, & Bakermans-Kranenburg, 2010). Moreover, following oxytocin administration, fathers have been found to be more sensitive to a disruption in the interaction with their infants, as seen by increased cortisol levels during the face-to-face-still-face paradigm.

p.107

One of the mechanisms by which oxytocin is thought to facilitate prosocial caregiving behaviors is by reducing avoidance and the fear of novelty while enhancing acceptance of the infant (Carter, 1998). The study by Riem and colleagues provides some support for this hypothesis: men and women were administered oxytocin or a placebo and were then exposed to

an infant's signals of distress (crying sounds). The authors found that oxytocin administration reduced amygdala activation, a neural circuitry involved in aversion behaviors, and increased activation of the insula and inferior frontal gyrus, regions involved in empathic responses (Riem et al., 2011). In addition, the oxytocinergic system likely facilitates the initiation of caring motivation (Rilling, 2013) and promotes the protection of offspring (Rilling & Young, 2014) by virtue of its facilitating interactions with the reward-seeking mesolimbic dopaminergic neurons (Feldman, 2012).

Likewise, oxytocinergic-dopaminergic interactions might be central for creating caring compassionate motivation (Preston & Hofelich, 2012); ventral tegmental and ventral striatum dopamine areas have been found to activate when subjects adopt a compassionate stance when viewing photographs of others suffering (Kim et al., 2009). In addition, compassion-based meditation such as Loving Kindness Meditation (LKM) enhance neural responses to vignettes of others suffering in conjunction with ventral tegmental area activation (Klimecki, Leiberg, Lamm, & Singer, 2013).

The expression of compassionate behaviors relies on an increase in approach motivation in conjunction with reduced defensive avoidance motivation (Gilbert, 2010, 2014; see [Chapter 3](#)). The inclination to be caring and compassionate may be stronger in people we perceive as being pleasant than in those we perceive as being unpleasant. Oxytocin seems to impact this dimension. For example, intranasal administration of oxytocin appears to increase the attractiveness of infant faces (Marsh et al., 2012) and to enhance the attractiveness of unfamiliar faces (Theodoridou, Rowe, Penton-Voak, & Rogers, 2009). One possible underlying mechanism by which oxytocin could exert such an impact on the perception of pleasantness is in regulating amygdala activity and reducing the perceived ambiguity regarding the valence of social stimuli, and promoting approach behavior, thus facilitating affiliation (Domes et al., 2007).

Furthermore, central oxytocin regulates bodily functions associated with the parasympathetic nervous system by modulating output from the vagal dorsal motor nucleus (Carter, 2014). Vagus nerve activity is of particular importance to emotional regulation and social engagement (Porges, 2003). Oxytocin administration has been found to increase heart-rate variability (HRV) in humans at rest in the absence of any external demands on participants (Kemp et al., 2012). These vagal and oxytocin mediated mechanisms, by which withdrawal-related behaviors are inhibited and approach-related social behaviors (social engagement) are enhanced, may contribute to the expression of compassionate responses.

p.108

Caring compassion motivation leads to prosocial behaviors that may contribute to preventing and alleviating others' suffering. The instrumental support is one of the expressions of compassionate prosocial behavior (Gilbert, 2010). Oxytocin has been found to influence instrumental social support. Specifically, a single administration of oxytocin nasal spray increases a person's willingness to share their own economic resources with a deprived child, with no expectation for reciprocation. Interestingly, these effects were mediated by levels of parental love-withdrawal. Participants reporting supportive backgrounds were more willing to act in a prosocial manner than women reared in more families that were less supportive emotionally (Van IJzendoorn, Huffmeijer, Alink, Bakermans-Kranenburg, & Tops, 2011).

In line with the findings of Van IJzendoorn and colleagues, a study by Riem and colleagues (Riem, Bakermans-Kranenburg, Huffmeijer, & van IJzendoorn, 2013) found that oxytocin facilitates compassionate prosocial behavior toward socially excluded individuals in a Cyberball social exclusion game. The tendency to compensate for other players' ostracism was enhanced after oxytocin administration, but only in participants with low levels of maternal love withdrawal (Riem et al., 2013).



## Oxytocin's role in feelings of safeness, and the mediating role of attachment style

Compassion Focused Therapy enhances feelings of comfort and safeness, and the associated inclination to positively relate to oneself, while feeling socially safe with others (Gilbert, 2010; Petrocchi, Ottaviani, & Couyoumdjian, 2016). The oxytocinergic system has been found to be involved in the expression of such feelings; specifically, oxytocin administration reduces feelings associated with separation distress (Panksepp, 2009), increases a positive view of oneself (Colonnello & Heinrichs, 2014) and promotes a positive perception of social aspects of the self (Cardoso, Ellenbogen, & Linnen, 2012). In addition, oxytocinergic system activation is associated with feelings of safeness and belonging, typical of secure attachment bonds. For example, in a study by Buchheim and colleagues (2009), men with insecure attachment patterns were asked to view pictures representing attachment-related events (e.g. a girl looking outside a window) accompanied by several statements representing the established attachment categories: secure, insecure-dismissing, insecure-preoccupied and unresolved trauma or loss. Each picture was accompanied by four statements, one for each attachment category. The participants were instructed to rank the statement based on its appropriateness to the picture. Participants reported a greater experience of attachment security following oxytocin, but not upon placebo administration. Notably, most but not all (69%) of the participants benefited from oxytocin administration, which highlights the individual variability in the oxytocinergic system's activity. Would oxytocin induce similar effects when the individuals with insecure attachment style were asked to recollect their own personal memories of caregiving figures or to imagine, *hic et nunc*, interactions with a positive caregiving figure? The study by Bartz and colleagues suggests that this is not the case. While oxytocin facilitates the recollection of positive maternal care and closeness in individuals with less anxious attachment patterns, it enhances the recollection of the mother *as less caring* after oxytocin (*versus the placebo*) in individuals with higher anxious attachment patterns (Bartz et al., 2010).

Notably, the effects of the increase in central oxytocin levels via nasal administration are dependent on context and the individual's attachment style (Bartz, Zaki, Bolger, & Ochsner, 2011). The availability of a perceived positive caring environment during throughout the individual's development contributes to shaping the brain's oxytocinergic system in humans and the body's sensitivity/responses to oxytocin administration in adulthood. In conjunction, the availability and quality of parental care in childhood contributes to the organization of long-term oxytocinergic function. For example, Fries and colleagues (2005) found a relationship between social experience in infancy and urinary oxytocin levels in childhood: compared to children reared by their biological parents, children who had been institutionalized or adopted had lower oxytocin levels (Fries, Ziegler, Kurian, Jacoris, & Pollak, 2005).

It has been suggested that epigenetic processes might lead to lowered oxytocin sensitivity: parental rejection might raise methylation levels and thereby suppress genetic expression in areas related to the oxytocinergic system, thus decreasing receptiveness to intranasal oxytocin administration (van IJzendoorn, Bakermans-Kranenburg, & Ebstein, 2011). These findings form a good link with attachment studies showing that insecure attachment style is associated with reduced prosocial behavior (Mikulincer, Orbach, & Iavnieli, 1998; Mikulincer & Shaver, [Chapter 11](#), this volume) and with compassion studies reporting the moderating role of attachment style on the effects of imagining a compassionate figure.

Rockliff et al. (2011) explored the effects of oxytocin on compassion-focused imagery (CFI) – that is, imagining another person being deeply compassionate to oneself – and the interaction of these effects with attachment security, self-criticism and feeling socially safe with others.

Oxytocin increased the ease of imagining compassionate qualities; however, participants lower in attachment security, self-reassurance and social safety, and higher in self-criticism, had less-positive CFI experiences with oxytocin than with a placebo, indicating that the effects of oxytocin on affiliation may depend on one's attachment and self-evaluative style. In line with the "social salience hypothesis," oxytocin alters the perceptual salience and processing of social cues, thus creating a different effect on individuals depending on their dispositional traits and interpersonal situation (Bartz et al., 2011; Shamay-Tsoory & Abu-Akel, 2016).

Taken together, these findings suggest that a single dose of oxytocin may facilitate the encoding of specific attachment-related events and the recollection, acceptance and sharing of one's own negative memories, imagery and feelings, rather than modifying the attachment representation itself. Thus, high oxytocin levels would be relevant in a clinical context because oxytocin would give patients access to neglected or suppressed emotional memories and open the individual to the possibility of sharing. This sheds light on a phenomenon observed by Bowlby and described by Gilbert (2009, 2010) whereby positive feelings generated by caring interactions (for example a therapist being kind and reassuring with the client) might be experienced by the client as extremely frightening, thus activating a defensive response. It is possible that increased oxytocin generated by cues of kindness from the therapist would facilitate the activation of negative attachment-related memories in subjects with insecure attachment patterns. This is congruent with findings from recent studies indicating that oxytocin increases the ability to express one's own emotions (Lane et al., 2013), such as self-reported feelings of sadness in postnatally depressed mothers (Mah, Van IJzendoorn, Smith, & Bakermans-Kranenburg, 2013), while increasing the salience of social stimuli, as discussed in the next section.

p.110

## Oxytocin and emotional understanding

Compassionate behavior is the ultimate output of the processing of information regarding one's own resources and feelings of safeness and the understanding of another person's perspective. To provide the kind of support that is more efficient to the care-elicitor, understanding another person's emotions and perspective is crucial. Notably, the emotion-recognition ability has been linked to prosocial behavior (Marsh, Kozak, & Ambady, 2007).

Several studies indicate that the neuropeptide oxytocin enhances the ability to detect other people's emotional expressions and recognize them accurately (Shahrestani, Kemp, & Guastella, 2013). For example, in the study by Schulze et al. (2011), participants were asked to indicate the presence or absence of target angry and happy faces versus neutral distractors. These were presented for 18, 35, or 53 ms and then subsequently masked by neutral faces. The authors found that oxytocin enhances the accuracy of detecting emotional faces, especially happy faces. Oxytocin has consistently been found to increase the shift of attention towards happy facial expressions at the early stage of face processing (100 ms) on a dot-probe paradigm, without affecting overt visual attention (Domes et al., 2013). Moreover, oxytocin administration reduced the activity of the anterior amygdala laterally and dorsally for fearful emotional faces, while increasing the activity for happy facial expressions on an emotion classification task (Gamer, Zurowski, & Büchel, 2010).

The facilitating effect of oxytocin for detecting positive social cues, such as happy facial expressions, is coupled with reduced reactivity to threatening social cues. For example, intranasal oxytocin administration weakens neural correlation of early arousal while viewing threat cues from the eyes (Kanat, Heinrichs, Schwarzwald, & Domes, 2015). Apparently, the enhanced ability to recognize positive emotions seems to contradict the thesis that



compassionate behavior is based on recognizing another's suffering. However, this apparent paradox could easily be understood if one considers that the final goal of compassionate motivation is not only to *approach* suffering (modulating the level of arousal induced by negative emotions without impairing their recognition), but also to *promote* and sustain other's positive emotions. The early detection of positive emotions, facilitated by the oxytocinergic system, is important to bond formation and to guide, positively reinforce and maintain compassion-focused behavior.

As highlighted above, the effects of oxytocin administration depend on an individual's traits. For example, oxytocin administration increases a person's attention to facial stimuli, as indicated by relative greater pupil dilation in participants with low emotional sensitivity (Leknes et al., 2012). Riem and colleagues (2014) found that oxytocin increases the ability to recognize another's emotion in the Reading the Mind in the Eyes Test (RMET), a task in which participants are presented with emotions revealing varying difficulty of degrees to be recognized. This effect was stronger in participants reporting higher levels of maternal love withdrawal.

p.111

## Polymorphisms of the OX gene

The effects of oxytocin administration on emotion recognition ability are also influenced by the oxytocin receptor gene's variation (see Conway & Slavich, [Chapter 9](#), this volume). Polymorphisms have been identified for a number of neurotransmitter systems and one impact of them is contribute to individual sensitivity to the environment. For example, a six-marker haplotype block (the TTCGGG haplotype comprising single-nucleotide polymorphisms rs237917–rs2268498–rs4564970–rs237897–rs2268495–rs53576) is associated with increased emotion recognition ability following oxytocin compared with placebo administration. By contrast, the CCGAGA haplotype showed the opposite pattern (Chen et al., 2015).

A crucial ability found to be influenced by oxytocin administration is the ability to represent, interpret, and understand the mental states of others, that is, the Theory of Mind (ToM). It has been suggested that a better ToM ability helps individuals account for others' feelings and desires and therefore leads to more compassionate behavior ([Chapter 3](#), this volume; Gilbert, 2010; Goldstein & Winner, 2012). Interestingly, twin studies suggest that large variance in children's ToM and prosocial behavior could be attributed to genetic factors (Hughes, Jaffee, Taylor, Caspi, & Moffit, 2005). The oxytocin receptor gene (OXTR) is one of the major candidates in explaining different subtypes of prosocial behavior. In a recent study on children (Wu & Su, 2015), oxytocin receptor (OXTR) variations were able to predict the difference in both prosocial behaviors and ToM ability: individuals homozygous for the G allele (GG; OXTR rs53576 genotype) exhibited more prosocial behaviors (increased helping and comforting, but not sharing) and better ToM ability than other genotypes.

The link between oxytocin and ToM has also been reported in mothers. A recent longitudinal study on pregnant women found that the level of plasma oxytocin during late pregnancy predicted increased ToM abilities, which in turn was associated with less remote and less depressive maternal interactive behavior during the first post-partum trimester (MacKinnon et al., 2014). Thus, alterations in the oxytocinergic system during the perinatal period may contribute to the awareness of social cues, which in turn has an impact on maternal interactive behavior. We also know that intranasal administration of oxytocin improves ToM in healthy men (Domes, Heinrichs, Michel, Berger, & Herpertz, 2007) and individuals with autism spectrum disorders (Guastella et al., 2010).

These findings suggest endogenous oxytocin may be a biomarker of social motivation and of individual sensitivity to social cues (Bartz et al., 2011), and could explain variability in the efficacy of compassion focus therapies.

p.112

## Oxytocin and self/other distinction

Compassionate behavior is characterized by a prosocial approach, which implies the ability to tune or synchronize with others while maintaining the self/other distinction. In fact, as suggested by research from social psychology, excessive overlap between the “self” and “other” may produce personally oriented distress that leads to emotional disengagement, rather than compassionate behavior (Batson & Shaw, 1991). The development of a distinct self-concept is connected with a child’s propensity to make helpful advances toward others (Hoffman, 2001).

Based on this data, social cognitive neuroscience research identifies the self/other distinction as a key component of empathy (Lamm, Bukowski, & Silani, 2016) and compassion. Oxytocin administration has been found to increase the tendency to synchronize one’s own behavior with another’s behavior (De Coster, Mueller, T’Sjoen, De Saedeleer, & Brass, 2014), while it increases the tendency to distinguish from self- and other-related stimuli (Colonnello et al., 2013). High central oxytocin levels facilitate the recognition of the self/other distinction. Specifically, compared to placebo administration, intranasal oxytocin administration shortened the time it took to recognize the identity in a self/other recognition task in which the photo of the participant’s face morphed into the photo of an unfamiliar individual’s face and vice versa. Regardless of the morphing direction, participants who received oxytocin demonstrated an advantage in recognizing their own and unfamiliar facial features. Notably, participants who received oxytocin were also more likely than placebo-treated participants to evaluate others positively (Colonnello et al., 2013). By dampening fear responses and enhancing dopaminergic-mediated seeking motivation, oxytocin may facilitate the recognition and acceptance of self/other differences.

Other studies have continued to explore the idea that oxytocin might be involved in self/other distinction processing. For example, Zhao et al. (2016) investigated the effect of oxytocin administration on judgment and the recollection of self (and other) (mother, classmate, or stranger) traits. Oxytocin has been found to accelerate the speed of decisions for the self versus other trait judgments. Thus, the work by Zhao and colleagues, expanding upon previous results on oxytocin effects on the self/other distinction, suggests that the effects of oxytocin on self/other distinction judgments are specific to the initial phases of self/other approach/interactions (Zhao et al., 2016).

p.113

In another analysis that aimed to study the link between oxytocin, the self/other distinction and empathic ability, participants received oxytocin or placebo and then were asked to imagine themselves (self-condition) and other individuals (other condition) in painful and non-painful situations. While no differences between the self and other conditions were found following placebo administration, oxytocin administration increased empathy to pain when imaging others, but not the self, in a painful condition (Abu-Akel, Palgi, Klein, Decety, & Shamay-Tsoory, 2015). Taken together, these results suggest that oxytocin might contribute to promoting feelings of compassion by reducing personal distress, sharpening the self/other distinction, and enhancing the understanding of others’ needs.

Appearing to contrast with these studies on oxytocin’s effect on sharpening self/other distinction, some have found that oxytocin administration increases self/other integration

performance during a joint/social Simon task (Ruissen & de Bruijn, 2015) and decreases the control over automatic imitative behavior in a motor simulation task (De Coster et al., 2014). It is possible that one of the mechanisms by which oxytocin facilitates the recognition of self/other differences and the understanding of another's perspective is by increasing self/other motor tuning. From an evolutionary perspective, oxytocin-driven caring behavior relies on the caregiver's ability to both tune into the infant/care-elicitor and maintain the self/other distinction to realize effective caring behaviors. However, the temporal processing of self/other merging and distinguishing under increased oxytocin levels is unknown.

Interestingly, mindfulness and compassion-based psychotherapy approaches such as Compassion Focused Therapy (Gilbert, 2010) highlight the importance of helping patients to positively relate to others and to recognize and accept the presence of "multiple selves," that is, the different patterns of cognitive, emotional and motivational processing in oneself that can be "observed" with a curious, kindly observing stance, as if the personality of another, distinct individual were being manifested. This practice seems to facilitate a better understanding of, and healthy distinction from, difficult mental states that can be experienced and held in a more compassionate and less self-critical and distressing manner. In fact, there is evidence that the soothing effect of self-compassion practices can be strengthened with the use of a mirror that "externalizes" the object of the compassion practice (Petrocchi et al., 2016). Whether oxytocin promotes the soothing effect of this kind of compassion-focused practices remains unexplored.

Oxytocin's effects on the self/other distinction extend to the social ingroup-outgroup. Several studies by De Dreu and colleagues corroborate the role of this neurohormone in mediating the self/other distinction. Such a distinction does not necessarily lead to outgroup withdrawal. For example, oxytocin administration enhances cooperative behaviors within and between groups (Israel, Weisel, Ebstein, & Bornstein, 2012), increases social conformity under implicit social pressure (Huang, Kendrick, Zheng, & Yu, 2015), and facilitates care for individuals considered to be self-related (ingroup members), without necessarily inducing outgroup derogation (De Dreu, Greer, Van Kleef, Shalvi, & Handgraaf, 2011) or withdrawal to antagonists (Ten Velden, Baas, Shalvi, Kret, & De Dreu, 2014).

Oxytocin may, by enhancing self-confidence (Colonnello & Heinrichs, 2014), regulate prosocial behavior by limiting it to cooperative outgroup members (De Dreu, Shalvi, Greer, Van Kleef, & Handgraaf, 2012), facilitate approach motivation and the affiliation towards individuals perceived as physically strong (Chen, Mayer, Mussweiler, & Heinrichs, 2015; DeDreu, Greer, Handgraaf, Shalvi, & Van Kleef, 2012) and enhance ingroup-bias in individuals with a cognitive style characterized by inclination toward intuition rather than reflection (Ma, Liu, Rand, Heatherton, & Han, 2015).

p.114

## Conclusion

Compassion is considered the expression of the extended caregiving system that motivates individuals to regulate their own self-defense mechanisms to approach others in distress, and promotes the well-being of non-kin members in society. The oxytocinergic system appears involved in modulating certain aspects of compassion motivation and compassion-related feelings and behaviors. As reviewed here, oxytocin promotes caring inclination and enhances the ability to understand another's perspective while maintaining the self/other distinction. In addition, oxytocin administration promotes social support towards socially excluded individuals which – from the perspective of compassion studies – is particularly relevant considering that (as Goetz et al., 2010, highlighted) the appraisal of vulnerability seems to be central to triggering the motivational state of compassion.

All this evidence suggests that the activation of this system is likely to be involved in the expression of compassion-related feelings and behaviors. However, several questions need to be addressed to better understand the role of oxytocin in compassion motivation. For example, it would be worth investigating whether increased oxytocin levels enhance the ability to adopt compassionate approach behavior despite perceived self/other differences. In addition, the temporal processing of self/other merging and distinction under increased oxytocin levels during compassion-focused therapy deserves research attention.

Furthermore, future research should investigate whether oxytocin, facilitating the self/other distinction, has a role to play in promoting accepting feelings towards the rejected aspects of self during compassion-focused practices, and to what extent this is mediated by an individual's personality traits and genetic variations in the oxytocin system. Compassion is obviously a complex phenomenon that most likely relies on the activation of more than one system and whose behavioral expressions are dependent on context. Thus, future studies should investigate the interactions between oxytocinergic, dopaminergic, and opiodergic systems in enhancing feeling of safeness in compassion-focused therapies.

p.115

## References

- Abu-Akel, A., Palgi, S., Klein, E., Decety, J., & Shamay-Tsoory, S. (2015). Oxytocin increases empathy to pain when adopting the other- but not the self-perspective. *Social Neuroscience, 10*, 7–15.
- Bartz, J. A., Zaki, J., Bolger, N., & Ochsner, K. N. (2011). Social effects of oxytocin in humans: Context and person matter. *Trends in Cognitive Sciences, 15*, 301–309.
- Bartz, J. A., Zaki, J., Ochsner, K. N., Bolger, N., Kolevzon, A., Ludwig, N., & Lydon, J. E. (2010). Effects of oxytocin on recollections of maternal care and closeness. *Proceedings of the National Academy of Sciences, 107*, 21371–21375.
- Batson, C. D., & Shaw, L. L. (1991). Evidence for altruism: Toward a pluralism of prosocial motives. *Psychological Inquiry, 2*, 107–122.
- Buchheim, A., Heinrichs, M., George, C., Pokorny, D., Koops, E., Henningsen, P., . . . Gündel, H. (2009). Oxytocin enhances the experience of attachment security. *Psychoneuroendocrinology, 34*, 1417–1422.
- Cardoso, C., Ellenbogen, M. A., & Linnen, A. M. (2012). Acute intranasal oxytocin improves positive self-perceptions of personality. *Psychopharmacology, 220*, 741–749.
- Carter, C. S. (1998). Neuroendocrine perspectives on social attachment and love. *Psychoneuroendocrinology, 23*, 779–818.
- Carter, C. S. (2014). Oxytocin pathways and the evolution of human behavior. *Annual Review of Psychology, 65*, 17–39.
- Chen, F. S., Kumsta, R., Dvorak, F., Domes, G., Yim, O. S., Ebstein, R. P., & Heinrichs, M. (2015). Genetic modulation of oxytocin sensitivity: a pharmacogenetic approach. *Translational Psychiatry, 5*, 664.
- Chen, F. S., Mayer, J., Mussweiler, T., & Heinrichs, M. (2015). Oxytocin increases the likeability of physically formidable men. *Social Cognitive and Affective Neuroscience, 10*, 797–800.
- Colonnello, V., Chen, F. S., Panksepp, J., & Heinrichs, M. (2013). Oxytocin sharpens self-other perceptual boundary. *Psychoneuroendocrinology, 38*, 2996–3002.
- Colonnello, V., Domes, G., & Heinrichs, M. (2016). As time goes by: Oxytocin influences the subjective perception of time in a social context. *Psychoneuroendocrinology, 68*, 69–73.

- Colonnello, V., & Heinrichs, M. (2014). Intranasal oxytocin enhances positive self-attribution in healthy men. *Journal of Psychosomatic Research*, *77*, 415–419.
- Colonnello, V., Petrocchi, N., Farinelli, M., & Ottaviani, C. (2016). Positive social interactions in a lifespan perspective with a focus on opioidergic and oxytocinergic systems: Implications for neuroprotection. *Current Neuropharmacology*, in press.
- De Coster, L., Mueller, S. C., T'Sjoen, G., De Saedeleer, L., & Brass, M. (2014). The influence of Oxytocin on automatic motor simulation. *Psychoneuroendocrinology*, *50*, 220–226.
- De Dreu, C. K., Greer, L. L., Handgraaf, M. J., Shalvi, S., & Van Kleef, G. A. (2012). Oxytocin modulates selection of allies in intergroup conflict. *Proceedings of the Royal Society B*, *279*, 1150–1154.
- De Dreu, C. K., Greer, L. L., Van Kleef, G. A., Shalvi, S., & Handgraaf, M. J. (2011). Oxytocin promotes human ethnocentrism. *Proceedings of the National Academy of Sciences*, *108*, 1262–1266.

p.116

- De Dreu, C. K., Shalvi, S., Greer, L. L., Van Kleef, G. A., & Handgraaf, M. J. (2012). Oxytocin motivates non-cooperation in intergroup conflict to protect vulnerable in-group members. *PLOS ONE*, *7*, e46751.1.
- Ditzen, B., Schaer, M., Gabriel, B., Bodenmann, G., Ehlert, U., & Heinrichs, M. (2009). Intranasal oxytocin increases positive communication and reduces cortisol levels during couple conflict. *Biological Psychiatry*, *65*, 728–731.
- Domes, G., Heinrichs, M., Glascher, J., Buchel, C., Braus, D. F., & Herpertz, S. C. (2007). Oxytocin attenuates amygdala responses to emotional faces regardless of valence. *Biological Psychiatry*, *62*, 1187–1190.
- Domes, G., Heinrichs, M., Michel, A., Berger, C., & Herpertz, S. C. (2007). Oxytocin improves “mind-reading” in humans. *Biological Psychiatry*, *61*, 731–733
- Domes, G., Sibold, M., Schulze, L., Lischke, A., Herpertz, S. C., & Heinrichs, M. (2013). Intranasal oxytocin increases covert attention to positive social cues. *Psychological Medicine*, *43*, 1747–1753.
- Donaldson, Z. R., & Young, L. J. (2008). Oxytocin, vasopressin, and the neurogenetics of sociality. *Science*, *322*, 900–904.
- Feldman, R. (2012). Oxytocin and social affiliation in humans. *Hormones and Behavior*, *61*, 380–391.
- Feldman, R., Gordon, I., Schneiderman, I., Weisman, O., & Zagoory-Sharon, O. (2010). Natural variations in maternal and paternal care are associated with systematic changes in oxytocin following parent–infant contact. *Psychoneuroendocrinology*, *35*, 1133–1141.
- Feldman, R., Gordon, I., & Zagoory-Sharon, O. (2011). Maternal and paternal plasma, salivary, and urinary oxytocin and parent–infant synchrony: Considering stress and affiliation components of human bonding. *Developmental Science*, *14*, 752–761.
- Feldman, R., Weller, A., Zagoory-Sharon, O., & Levine, A. (2007). Evidence for a neuroendocrinological foundation of human affiliation plasma oxytocin levels across pregnancy and the postpartum period predict mother-infant bonding. *Psychological Science*, *18*, 965–970.
- Fries, A. B. W., Ziegler, T. E., Kurian, J. R., Jacoris, S., & Pollak, S. D. (2005). Early experience in humans is associated with changes in neuropeptides critical for regulating social behavior. *Proceedings of the National Academy of Sciences of the United States of America*, *102*, 17237–17240.



- Galbally, M., Lewis, A. J., IJzendoorn, M. V., & Permezel, M. (2011). The role of oxytocin in mother-infant relations: a systematic review of human studies. *Harvard Review of Psychiatry, 19*, 1–14.
- Gamer, M., Zurowski, B., & Büchel, C. (2010). Different amygdala subregions mediate valence-related and attentional effects of oxytocin in humans. *Proceedings of the National Academy of Sciences, 107*, 9400–9405.
- Gilbert, P. (2009). Introducing compassion-focused therapy. *Advances in Psychiatric Treatment, 15*, 199–208.
- Gilbert, P. (2010). An introduction to compassion focused therapy in cognitive behavior therapy. *International Journal of Cognitive Therapy, 3*, 97–112.
- Gilbert, P. (2014). The origins and nature of compassion focused therapy. *British Journal of Clinical Psychology, 53*, 6–41.
- Gilbert, P. (2015). The Evolution and Social Dynamics of Compassion. *Social and Personality Psychology Compass, 9*, 239–254.
- Goetz, J. L., Keltner, D., & Simon-Thomas, E. (2010). Compassion: An evolutionary analysis and empirical review. *Psychological Bulletin, 136*, 351–374

p.117

- Goldstein, T. R., & Winner, E. (2012). Enhancing empathy and theory of mind. *Journal of Cognition and Development, 13*, 19–37.
- Guastella, A. J., Einfeld, S. L., Gray, K. M., Rinehart, N. J., Tonge, B. J., Lambert, T. J., & Hickie, I. B. (2010). Intranasal oxytocin improves emotion recognition for youth with autism spectrum disorders. *Biological Psychiatry, 67*, 692–694.
- Hoffman, M. L. (2001). *Empathy and Moral Development: Implications for Caring and Justice*. New York: Cambridge University Press.
- Huang, Y., Kendrick, K. M., Zheng, H., & Yu, R. (2015). Oxytocin enhances implicit social conformity to both in-group and out-group opinions. *Psychoneuroendocrinology, 60*, 114–119.
- Hughes, C., Jaffee, S. R., Taylor, A., Caspi, A., & Moffit, T. E. (2005). Origins of individual difference in theory of mind: From nature to nurture? *Child Development, 76*, 356–370.
- Israel, S., Weisel, O., Ebstein, R. P., & Bornstein, G. (2012). Oxytocin, but not vasopressin, increases both parochial and universal altruism. *Psychoneuroendocrinology, 37*, 1341–1344.
- Kanat, M., Heinrichs, M., Schwarzwald, R., & Domes, G. (2015). Oxytocin attenuates neural reactivity to masked threat cues from the eyes. *Neuropsychopharmacology, 40*, 287–295.
- Kemp, A. H., Quintana, D. S., Kuhnert, R. L., Griffiths, K., Hickie, I. B., & Guastella, A. J. (2012). Oxytocin increases heart rate variability in humans at rest: Implications for social approach-related motivation and capacity for social engagement. *PLOS ONE, 7*, e44014.
- Kim, J.-W., Kim, S.-E., Kim, J.-J., Jeong, B., Park, C.-H., Son, A. R., . . . Ki, S.W. (2009). Compassionate attitude towards others' suffering activates the mesolimbic neural system. *Neuropsychologia, 47*, 2073–2081.
- Klimecki, O.M., Leiberg, S., Lamm, C., & Singer, T. (2013). Functional neural plasticity and associated changes in positive affect after compassion training. *Cerebral Cortex, 23*, 1552–1561.
- Lamm, C., Bukowski, H., & Silani, G. (2016). From shared to distinct self-other representations in empathy: Evidence from neurotypical function and socio-cognitive disorders. *Philosophical Transactions of the Royal Society B, 371*(1686), 20150083.
- Lane, A., Luminet, O., Rimé, B., Gross, J. J., de Timary, P., & Mikolajczak, M. (2013). Oxytocin increases willingness to socially share one's emotions. *International Journal of Psychology, 48*, 676–681.

- Leknes, S., Wessberg, J., Ellingsen, D. M., Chelnokova, O., Olausson, H., & Laeng, B. (2012). Oxytocin enhances pupil dilation and sensitivity to “hidden” emotional expressions. *Social Cognitive and Affective Neuroscience*, 8, 741–749.
- Ma, Y., Liu, Y., Rand, D. G., Heatherton, T. F., & Han, S. (2015). Opposing oxytocin effects on intergroup cooperative behavior in intuitive and reflective minds. *Neuropsychopharmacology*, 40, 2379–2387.
- MacKinnon, A. L., Gold, I., Feeley, N., Hayton, B., Carter, C. S., & Zelkowitz, P. (2014). The role of oxytocin in mothers’ theory of mind and interactive behavior during the perinatal period. *Psychoneuroendocrinology*, 48, 52–63.
- MacLean, P. D. (1985). Brain evolution relating to family, play, and the separation call. *Archives of General Psychiatry*, 42, 405–417.
- Mah, B. L., Van IJzendoorn, M. H., Smith, R., & Bakermans-Kranenburg, M. J. (2013). Oxytocin in postnatally depressed mothers: Its influence on mood and expressed emotion. *Progress in Neuro-Psychopharmacology and Biological Psychiatry*, 40, 267–272.

p.118

- Marsh, A. A., Henry, H. Y., Pine, D. S., Gorodetsky, E. K., Goldman, D., & Blair, R. J. R. (2012). The influence of oxytocin administration on responses to infant faces and potential moderation by OXTR genotype. *Psychopharmacology*, 224, 469–476.
- Marsh, A. A., Kozak, M. N., & Ambady, N. (2007). Accurate identification of fear facial expressions predicts prosocial behavior. *Emotion*, 7, 239–251.
- Meyer-Lindenberg, A., Domes, G., Kirsch, P., & Heinrichs, M. (2011). Oxytocin and vasopressin in the human brain: Social neuropeptides for translational medicine. *Nature Reviews Neuroscience*, 12, 524–538.
- Mikulincer, M., Orbach, I., & Iavnieli, D. (1998). Adult attachment style and affect regulation: Strategic variations in subjective self–other similarity. *Journal of Personality and Social Psychology*, 75, 436.
- Naber, F., van IJzendoorn, M. H., Deschamps, P., van Engeland, H., & Bakermans-Kranenburg, M. J. (2010). Intranasal oxytocin increases fathers’ observed responsiveness during play with their children: A double-blind within-subject experiment. *Psychoneuroendocrinology*, 35, 1583–1586.
- Panksepp, J. (1998). *Affective neuroscience: The foundations of human and animal emotions*. New York: Oxford University Press.
- Panksepp, J. (2009). Primary process affects and brain oxytocin. *Biological Psychiatry*, 65(9), 725–727.
- Panksepp, J., & Biven, L. (2012). *The archaeology of mind: Neuroevolutionary origins of human emotions (Norton series on interpersonal neurobiology)*. New York: W. W. Norton.
- Petrocchi, N., & Couyoumdjian, A. (2015). The impact of gratitude on depression and anxiety: The mediating role of criticizing, attacking, and reassuring the self. *Self and Identity*, 15(2), 191–205.
- Petrocchi, N., Ottaviani, C., & Couyoumdjian, A. (2016). Compassion at the mirror: Exposure to a mirror increases the efficacy of a self-compassion manipulation in enhancing soothing positive affect and heart rate variability. *The Journal of Positive Psychology*, 1–12.
- Porges, S. W. (2003). The polyvagal theory: Phylogenetic contributions to social behavior. *Physiology & Behavior*, 79, 503–513.
- Preston, S. D., & Hofelich, A. J. (2012). The many faces of empathy: Parsing empathic phenomena through a proximate, dynamic-systems view of representing the other in the self. *Emotion Review*, 4, 24–33.

- Riem, M. M., Bakermans-Kranenburg, M. J., Huffmeijer, R., & van IJzendoorn, M. H. (2013). Does intranasal oxytocin promote prosocial behavior to an excluded fellow player? A randomized-controlled trial with Cyberball. *Psychoneuroendocrinology*, *38*(8), 1418–1425.
- Riem, M. M., Bakermans-Kranenburg, M. J., Pieper, S., Tops, M., Boksem, M. A., Vermeiren, R. R., van IJzendoorn, M. H., & Rombouts, S. A. (2011). Oxytocin modulates amygdala, insula, and inferior frontal gyrus responses to infant crying: A randomized controlled trial. *Biological Psychiatry*, *70*, 291–297.
- Riem, M. M., Bakermans-Kranenburg, M. J., Voorthuis, A., & van IJzendoorn, M. H. (2014). Oxytocin effects on mind-reading are moderated by experiences of maternal love withdrawal: An fMRI study. *Progress in Neuro-Psychopharmacology and Biological Psychiatry*, *51*, 105–112.
- Rilling, J. K. (2013). The neural and hormonal bases of human parental care. *Neuropsychologia*, *51*, 731–747.

p.119

- Rilling J. K., & Young L. J. (2014). The biology of mammalian parenting and its effect on offspring social development. *Science*, *345*, 771–776.
- Rockliff, H., Karl, A., McEwan, K., Gilbert, J., Matos, M., & Gilbert, P. (2011). Effects of intranasal oxytocin on ‘compassion focused imagery’. *Emotion*, *11*, 1388–1396.
- Ruissen, M. I., & de Bruijn, E. R. (2015). Is it me or is it you? Behavioral and electrophysiological effects of oxytocin administration on self-other integration during joint task performance. *Cortex*, *70*, 146–54.
- Schulze, L., Lischke, A., Greif, J., Herpertz, S. C., Heinrichs, M., & Domes, G. (2011). Oxytocin increases recognition of masked emotional faces. *Psychoneuroendocrinology*, *36*, 1378–1382.
- Shahrestani, S., Kemp, A. H., & Guastella, A. J. (2013). The impact of a single administration of intranasal oxytocin on the recognition of basic emotions in humans: A meta-analysis. *Neuropsychopharmacology*, *38*, 1929–1936.
- Shahrokh, D. K., Zhang, T. Y., Diorio, J., Gratton, A., & Meaney, M. J. (2010). Oxytocin-dopamine interactions mediate variations in maternal behavior in the rat. *Endocrinology*, *151*, 2276–2286.
- Shamay-Tsoory, S. G., & Abu-Akel, A. (2016). The social salience hypothesis of oxytocin. *Biological Psychiatry*, *79*, 194–202.
- Ten Velden, F. S., Baas, M., Shalvi, S., Kret, M. E., & De Dreu, C. K. (2014). Oxytocin differentially modulates compromise and competitive approach but not withdrawal to antagonists from own vs. rivaling other groups. *Brain Research*, *1580*, 172–179.
- Theodoridou, A., Rowe, A. C., Penton-Voak, I. S., & Rogers, P. J. (2009). Oxytocin and social perception: Oxytocin increases perceived facial trustworthiness and attractiveness. *Hormones and Behavior*, *56*, 128–132.
- van IJzendoorn, M., Bakermans-Kranenburg, M., & Ebstein, R. (2011). Methylation matters in child development: Toward developmental behavioral epigenetics. *Child Development Perspectives*, *5*, 305–310.
- Van IJzendoorn, M. H., Huffmeijer, R., Alink, L. R., Bakermans-Kranenburg, M. J., & Tops, M. (2011). The impact of oxytocin administration on charitable donating is moderated by experiences of parental love-withdrawal. *Frontiers in Psychology*, *2*, 258.
- Wang, S. (2005). A conceptual framework for integrating research related to the physiology of compassion and the wisdom of Buddhist teachings. *Compassion: Conceptualisations, research and use in psychotherapy*, 75–120.



- Weisman, O., Zagoory-Sharon, O., & Feldman, R. (2012). Oxytocin administration to parent enhances infant physiological and behavioral readiness for social engagement. *Biological Psychiatry*, *72*, 982–989.
- Wu, N., & Su, Y. (2015). Oxytocin receptor gene relates to theory of mind and prosocial behavior in children. *Journal of Cognition and Development*, *16*, 302–313.
- Zhao, W., Yao, S., Li, Q., Geng, Y., Ma, X., Luo, L., . . . Kendrick, K. M. (2016). Oxytocin blurs the self-other distinction during trait judgments and reduces medial prefrontal cortex responses. *Human Brain Mapping*, *37*, 2512–2527.