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**IMPORTANT:** December 2010, Volume 25, Number 4, was the LAST ISSUE of the *Human Ethology Bulletin* to be distributed in hard (paper) copy over regular post. All copies are now being distributed electronically over email. If you were previously receiving paper copies, please be sure that the Membership Chair, Astrid Jütte (astrid.juette@gmx.net) has your email address.
Human Ethology Bulletin, 26(1), 2011

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Human Ethology Bulletin: An Online Peer-Reviewed Journal

Bulletin Policies

Starting with this first issue of 2011, the Human Ethology Bulletin is transforming into an online peer-reviewed journal. The paper (printed) version of the Human Ethology Bulletin has been discontinued, and fully electronic production and distribution formats have been adopted.

This journal will publish empirical, theoretical, and review articles broadly within the research tradition of Human Ethology, some of whose distinct features are described below. Human Ethology Bulletin will continue to publish book reviews and educational pieces. It will also invite papers on which peer commentaries are published.

Of particular interest will be studies where behavior is directly observed and recorded using a variety of methods which might range from traditional ad libitum direct observation in natural habitats to automatic computer-aided behavior recording and analysis. Scientific research programs are not set in stone, they evolve, and papers informed by the ethological approaches which extend or even challenge it will also be sympathetically considered. Whilst the focus is human behavior, papers on other species which have relevance to human behavior are welcomed. The various announcements specific to the internal business of the International Society for Human Ethology (ISHE), which used to appear in the Bulletin, will be moved to the recently enhanced ISHE web site and/or distributed via email.

Renewed Call for Papers

The previous calls for papers published in the Human Ethology Bulletin, and distributed over several electronic mailing lists, have emphasized the elucidation of the unique content which we hope to attract, and have actually begun to attract, to this journal. Due to numerous queries regarding the more technical and practical parameters of specific instructions to authors regarding submissions, we have developed a set of tentative guidelines for the different types of work that we will consider for publication.

We will consider the following types of submissions:

- **Research Articles** (up to ~10000 words, including references, notes and captions) are expected to present a major advance. Research Articles include an abstract, an introduction, up to six figures or tables, sections with brief subheadings, and up to a maximum of about 40 references.

- **Theoretical Reviews** (up to ~10000 words, including references, notes and captions) describe new developments of interdisciplinary significance and highlight future directions. They include an abstract, an introduction that outlines the main theme, brief subheadings, and an outline of important unresolved questions. A maximum of 40 references is suggested.

- **Target Articles** (up to ~10000 words, including references, notes and captions) must make theoretical or methodological interventions into current controversies within Human Ethology, broadly construed. Like Research Articles, Target Articles include an abstract, an introduction, up to six figures or tables, sections with brief subheadings, and about 40 references.

- **Open Peer Commentaries** (up to ~1000 words, including references, notes and
captions) consist of published, non-
anonymous commentaries on peer-
reviewed Target Articles from a dozen or
more specialists across disciplines, co-
published with the Author’s
Response. Open Peer Commentaries will be
solicited from the general readership (not by
special invitation, although commentaries
by some selected individuals might be
solicited by the Editor) upon the publication
of each Target Article for the next issue of
the Human Ethology Bulletin, and are due
six weeks after the publication of the Target
Article to leave sufficient time for peer
review.

- **Author’s Response to Open Peer
  Commentaries** (up to ~2500 words
  including references, notes and captions)
  will also be due six weeks after the
  publication of the Open Peer Commentaries
to leave sufficient time for peer review.

- **Brief Reports** (up to ~2500 words including
  references, notes and captions) present
  important new research results of broad
  significance. Reports should include an
  abstract, an introductory paragraph, up to
  four figures or tables, and up to a maximum
  of about 30 references.

- **Book Reviews** (up to 2000 words including
  references, notes and captions) present
  descriptions, evaluations, and critiques of
  new or recent books of theoretical,
  empirical, or practical importance to
  Human Ethology and related disciplines.
  Many Book Reviews are solicited by the
  editors, but unsolicited submissions are also
  considered.

- **Technical Comments** (up to 1000 words, 2
  figures or tables, and 15 references), are
  published in full and discuss research
  papers published in the *Human Ethology
  Bulletin* within the previous 12 months.
  Authors should submit a brief abstract (60
  words or less) to accompany their comment
  that will be included in the Letters section of
  the print edition. The authors of the original
  paper are given an opportunity to reply.
  Comments and responses are peer reviewed
  and edited as needed. Technical Comments
  posted elsewhere, in print or online,
  including on preprint servers, will generally
  not be considered.

- **Brevia** are brief contributions (500 to 1000
  words including references, notes and
  captions) accompanied by one illustration
  or table that must be contained on one
  printed page. Authors should also submit
  an abstract of 100 words or less that will
  appear online only.

**Present and Future Submissions**

For the time being, all submissions should be
formatted in APA style and should be sent
electronically as an attached Microsoft Word
2003 document to the Editor-in-Chief, Aurelio
José Figueredo, at ajf@u.arizona.edu. If email
submission is for some reason impossible,
hard copies may on occasion be accepted, as
long as they are accompanied by the same text
and graphics (where appropriate) on CD,
DVD, or USB drive.

All submissions must be in English. All
submissions, including invited contributions,
are subject to both peer and editorial review.
Some submissions are rejected, but political
censorship is avoided so as to foster free and
creative exchange of ideas among scholars. All
submissions should be original, and are not to
be published elsewhere, either prior to or after
publication in the *Bulletin*, without explicit
and prior permission from the Editor.

After that, the manuscript may be assigned to
a different Action Editor, selected from our
Editorial Board based on area of expertise.
These Action Editors will then send the
manuscripts out for peer review, and will be
contacting the authors directly regarding the outcomes of that process. Submitters may suggest peer reviewers that they believe would provide good critical evaluations, but the ultimate selection of reviewers will remain at the sole discretion of the specific Action Editor appointed to process each manuscript.

In the future, we will be moving to a fully web-based submission and review system. An excellent proposal has just been approved by the ISHE Board of Officers, so we might manage to have one in place as soon as the next (June) issue. However, these things take time and we cannot guarantee such immediate functionality.

When we do eventually adopt a fully web-based format, we may need to revise the posted guidelines so that the maximum word counts can be enforced electronically by the software. However, no automated software will ever be allowed to make the final decisions. If any contributing author believes that their submission merits an exception from these guidelines, they may write a letter of justification to the Editor, requesting such an exception. The letter has to clearly state the reasons that the extra word limit is required for adequate scientific communication, and the final decision will always be made by a living human being.

Disclaimer

The opinions expressed in the Human Ethology Bulletin, and any policy implications that might be inferred from them, do not necessarily reflect the views of the editorial staff or ISHE. Informed responses offering alternative views are welcome and can be sent directly to the Editor.

Reproduction

Material published in the Bulletin may be reproduced without limit for scholarly purposes but not for commercial activities. That is, Bulletin contents may not be reproduced in any form for profit unless prior permission is obtained from the Editor or the ISHE President. In all cases, the Human Ethology Bulletin or ISHE should be acknowledged, as appropriate (e.g., with a complete citation of source).

What is Human Ethology?

Human Ethology is, in some ways, distinct from other approaches to human behavior. Ethology has been defined as the biological study of behavior. Essentially, ethologists seek, first, through direct observation, to get a good description of their animal’s behavior in its natural habitat. For humans that habitat is extremely varied, from that of Hunter Gatherers in the forests of Papua New Guinea to that of office workers in a modern city like London.

Niko Tinbergen divided this one fundamental question into the so called “Four Questions”:

1. Proximate causation: What is the immediate causal mechanism within and outside the individual?
2. Ontogeny: What are the more distal causal influences in that individual’s development from conception onwards?
3. Function: What are the adaptive functions of that behavior, what is it good (or bad) for, how does it aid survival and reproduction?
4. Phylogeny: What is the evolutionary history of that behavior?

The Human Ethology Bulletin aims to provide a platform where more solid foundations for the study of human behavior may be published and discussed, together with developments arising out of that work, and thereby contribute to the development of a more reliable scientific understanding of human behavior.
Summer Institute in Human Ethology
Announcement
Prague, Czech Republic
5-9 July 2011

by Tom Alley, for the Program Committee

ISHE, together with Charles University, will sponsor a 2011 Summer Institute in Human Ethology. ISHE Summer Institutes have been developed to be more student-friendly than most scientific conferences, and include generous financial support for student participants (such as free registration and lodging for students who are first authors of accepted presentations). Previous ISHE summer institutes were held in Andechs, Germany (2007) and the University of Maine, U.S.A. (2009).

The 2011 meeting will be held 5 July (Tuesday p.m.) through 9 July (Saturday) at Charles University near the central area of Prague. Prague is the capital and largest city of the Czech Republic. Situated on the scenic Vltava River, Prague is home to many famous cultural, architectural and historical attractions. These combine to make the city one of the most popular tourist destinations in Europe. The extensive historic center of Prague is on the UNESCO list of World Heritage Sites. Tours of the Old Town or the Prague Zoo will be available to registrants on 9 July. A conference banquet will follow.

The institute is scheduled shortly after the 2011 HBES Conference (Montpelier, France, 29 June – 3 July) to allow more people to attend both meetings. The 2011 program will include invited speakers, student-oriented workshops, a poster session, and other presentations (see www.ISHE.org).

Invited speakers:
• Jay Belsky (Univ. of California-Davis, USA) – Keynote Speaker
• Jaroslav Flégr (Charles University: Czech Republic)
• S. Craig Roberts (University of Stirling, Scotland)
• Wulf Schiefenhövel (Max Planck Institute: Germany)

Workshops:
• Aurelio José Figueredo – How to apply life history theory to the study of human ethology: Evolution, genetics, development, measurement, and implications
• Jitka Lindová & Marc Méhu – Ethological analysis of nonverbal behaviour
• Jan Havlíček et al. – Performing research in human chemosignalling
• David Puts (Penn State) – Voice manipulation and analysis

Local arrangements:
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• Jan Havlíček – (Charles University, Prague, CZ)
• Daniel Kruger – (University of Michigan, MI, USA)
• Peter LaFreniere – (University of Maine, ME, USA)
• Elisabeth Oberzaucher – (University of Vienna, Austria)
This should be a fun and educational meeting for all. We hope you’ll be able to set aside a week in July to attend this meeting and enjoy one of the great cities of Europe. Further information, a registration system, and the call for submissions (reproduced below) are now posted on www.ISHE.org.

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Summer Institute in Human Ethology
Call for Submissions
Prague, Czech Republic
5-9 July 2011

by Tom Alley, for the Program Committee

Paper and poster proposals are now being sought for the 2011 Summer Institute on Human Ethology which will be held from Tuesday (evening), 5 July through Saturday, 9 July, in Prague, CZ.

I. General Information

Proposals for oral and poster presentations will be considered for inclusion in the program if they are received by 30 April 2011. Additional information about the Summer Institute is posted on the ISHE Web site: www.ISHE.org. All program participants, members, nonmembers, and students are expected to register for the meeting and pay the applicable registration fees. Students are particularly encouraged to attend and ISHE will provide generous financial subsidies for students presenting at the meeting.

II. Rules for Participation

1. Membership
It is not necessary to be a member of ISHE to submit a proposed program or presentation, and no preferential treatment will be given to submissions from ISHE members.

2. Number of Participations Allowed
Individuals are limited to two (2) presentations, with a maximum of one (1) oral presentation. This limit applies to the actual presentation of a paper in a paper or poster session. This does not include being a session chair or co-author.
who does not present, nor does participation in ISHE business meetings or as the presenter of an invited address.

3. Scheduling of Presentations
Persons with accepted presentations or programs must participate at the time scheduled by ISHE or arrange to have the presentation delivered by an appropriate substitute. Persons with time constraints for religious or other reasons must bring them to the attention of the Program Committee Chair (Tom Alley) when presentations are submitted or as soon as possible thereafter but before 20 May 2011.

4. Previously Published or Previously Read Presentations
Except by invitation, a presentation previously delivered at an ISHE meeting or other meeting for which one can expect overlap with the attendees at this Summer Institute (e.g., HBES, ISHE, EHBEA) may not be presented at the meeting unless it represents a substantial elaboration or revision (additional findings, etc.).

III. Guidelines and Procedures for Submitting Proposals

All proposals must be in English and submitted via the ISHE online Call for Submissions. The website is linked to ISHE’s website [www.ishe.org] under Summer Institutes. This website will guide you through the submission process for your individual and/or symposium proposals. Although the deadline for receipt of proposals is 30 April, 2011, early submission is strongly encouraged.

1. Presentation Types
The following types of presentations will be considered.

Submissions for individual presentations at the 2011 Summer Institute may be in the form of either oral papers or posters. Poster and paper presentations are governed by similar submission rules and review processes. For this meeting, students will be allowed to submit well-developed research proposals, such as one being developed for their dissertation, in poster format only. Submitters are encouraged to consider which format will work best for their particular presentation. Submitters may increase their chances of acceptance by indicating their willingness to deliver their presentation in either format; the Program Committee will then notify the applicant of the accepted format.

Papers:

Paper presentations will be allotted a minimum of 15 minutes for oral presentation, plus 5 minutes per paper added to the end of each session for discussion. Time constraints mean that this format may provide only limited opportunity for fully presenting one’s work and for interaction with attendees.

Posters:

ISHE encourages poster submissions so that research findings, new ideas, methodology and data analysis may be shared more fully and interactively. The poster session will allow presenters and attendees to engage in extended discussions regarding the author’s presentation that is in illustrated format on a poster board. For the Summer Institute we will accept student posters presenting a research plan as well as posters reporting the completed results of research by students or other scholars. It is anticipated that ISHE will provide at least two US$100 awards best poster awards.

Poster boards (950 x 1800 mm) and mounting tacks will be provided. If your submission is accepted for presentation as a poster, ISHE will send detailed instructions to assist you in preparing your materials in the required format.
2. General Instructions for All Paper and Poster Proposals

Each proposal must include the following:

1. Title of presentation – must not exceed 12 words

2. Name, e-mail address of person delivering presentation (principal author) complete mailing address, phone number, and affiliation (department, etc.). [In instances of multiple authorship, the person whose name is listed first normally is expected to deliver the presentation.]

3. Ordered list of the names and affiliation of all coauthors.

4. Preference for presentation in a poster session or in a paper session.

5. Summary of 150 to 300 words (not including Tables, Figures or references). The summary should include a statement of the problem or issue, methods and results (if an empirical proposal), and conclusions. For Research Proposal type posters, additional information about the rationale, background and methods may be provided in lieu of results and discussion. Note that this summary will be used for both review and, if successful, inclusion in the program guide.

Submit the proposal via the Summer Institute link on www.ISHE.org where additional information about the meeting can also be found.

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Smiling and Laughter in Naturally Occurring Dyadic Interactions: Relationship to Conversation, Body Contacts, and Displacement Activities

By Marc Méhu
Swiss Centre for Affective Sciences, University of Geneva

Abstract

Although research suggests that different types of smiles have different meaning, and possibly different functions, observational evidence to support that claim is relatively rare. The present study reports ethological observations on the frequency of smiling and laughter during naturally occurring dyadic interactions taking place in bars and cafés. Smiles were classified along two dimensions: spontaneous/deliberate and open/closed. Younger individuals displayed more laughter, spontaneous smiles and open smiles. People tended to smile more to individuals of their own sex and this was particularly salient for closed smiles, which appeared at significantly higher rates in male dyads. Different forms of smiles and laughter also varied with the behavioural context, characterized in this study by conversation time, displacement activities, and body contacts. The present findings also suggest that laughter plays a role in regulating partner's speech. This article supports the assumption that different forms of smiles have different functions in social relationships: Open and spontaneous smiles could be related to affiliation/bonding; whereas closed and deliberate smiles could be related to the regulation of status based social interactions. The relationship between smiling and laughter is also discussed.

Keywords: Smiling, Laughter, Smile Types, Conversation, Displacement Activities, Body Contact, Observational Study

Introduction

Building social relationships generally entails a series of interactions during which people are able to elicit the disclosure of valuable information by others and thereby acquire adaptive social knowledge. In order to achieve such a level of social expertise, people make use of a variety of information conveyed through diverse channels, including verbal exchanges and nonverbal cues (Grammer, Fivola, & Fieder, 1997). These different means of communication are believed to interact with each other to form a coherent system aimed at solving social issues such as mate choice (Grammer, 1989; Moore, 1985), social competition (Cashdan, 1998), or cooperation (Brown, Palameta, & Moore, 2003).

Smiling and laughter are ubiquitous in social interactions over the life time, starting from a very young age (Washburn, 1929; Wolff, 1963) and continuing into adulthood (Mehu & Dunbar, 2008a; Otta, 1998). Previous observations made distinctions between different forms of smiles based on the degree of mouth opening (Brannigan & Humphries, 1972) or the involvement of muscles in the eye region and particular movement dynamics (Duchenne de Boulogne, 1862; Ekman & Friesen, 1982). These different forms of smiles are believed to have different meanings (Ambadar, Cohn, & Reed, 2009; Ekman & Friesen, 1982; Otta, 1996) or functions (Mehu & Dunbar, 2008b). For example, the spontaneous smile, also known as the Duchenne smile (Ekman & Friesen, 1982), is believed to convey positive emotional experience such as joy (Frank, Ekman, & Friesen, 1997) and amusement (Ambadar et al., 2009), but also to
advertise altruistic intentions (Brown et al., 2003; Mehu, Grammer, & Dunbar, 1997). Moreover, the degree of mouth opening in smiling has been associated with increased levels of positive emotion (Ambadar et al., 2009; Messinger, Fogel, & Dickson, 2001; Otta, Abrosio, & Hoshino, 1996). The meaning usually attributed to other forms of smiles revolves around the themes of politeness, embarrassment, and nervosity (Ambadar et al., 2009; Goldenthal, Johnston, & Kraut, 1981; Keltner, 1995). Previous research therefore suggests that smiling may have different motivational bases and possibly different functions.

The role played by different forms of smiles in naturally occurring social interactions has generally been overlooked, as previous research mostly entailed rating studies of posed behaviour or investigations of facial displays recorded in constrained laboratory settings. Previous observational research showed that smiling and laughter could be involved in the formation of cooperative relationships (Mehu & Dunbar, 2008a) via the advertisement of prosocial dispositions (Brown et al., 2003; Mehu et al., 2007; Mehu, Little, & Dunbar, 2007; Tidd & Lockard, 1978). Although smiling and laughter were found to vary with ‘demographic’ factors such as group size or the age and sex of individuals involved (Adams & Kirkevold, 1978; Chapell, 1997; Mehu & Dunbar, 2008a), previous studies tell us little about the interactive mechanisms through which smiling and laughter could lead to social bonding.

The present study investigates the behavioural and social context of different forms of smiling and laughter as they appear in informal dyadic interactions. If smiling and laughter function to manage cooperative or competitive relationships they should be linked to a series of interpersonal behaviours that have been shown to occur repeatedly during affiliative and agonistic interactions. These behaviours are displacement activities, speaking and listening, and body contacts. Although they have been rarely studied in relation to smiling and laughter, these behavioural categories have been considered, in the psychological and ethological literature, as important regulators of social interactions.

Displacement activities form a class of non-verbal behaviours that is widely observed in human social interactions (Eibl-Eibesfeldt, 1989, p. 337; Ekman & Friesen, 1969; Morris, 1982, p. 277). These actions involve the manipulation of objects, clothes or body parts, auto-grooming, scratching, and self-touching, to name a few. The term displacement activity was first introduced by Tinbergen (1952) to describe behaviour that seemed irrelevant to the context in which it appears (Andrew, 1956; Tinbergen & van Iersel, 1948). For example, pecking movements in birds can be observed before or after a sexual fight, although these actions are relevant to foraging (Tinbergen, 1952). Displacement activities are expected to occur ‘when an activated motivation is denied discharge through its own consummatory act(s)’ (Tinbergen, 1952, p. 26). Tinbergen described two conditions in which this could happen: when there is a conflict between antagonist motivations, and when stimuli responsible for the release of a behaviour are absent.

Although displacement behaviours may not function as social signals, they are believed to reflect the state of tension or anxiety brought about by the social context (Maestripieri, Schino, Aureli, & Troisi, 1992). Generally speaking, social anxiety represents a condition of emotional arousal associated with the anticipation of danger (American Psychiatric Association, 1987; Watson & Friend, 1969). The ambiguity and uncertainty typical of social encounters is likely to provoke such tension. For example, the tension provoked by the conflicting tendencies to disclose relevant information to potential partners and to avoid
social exploitation by hiding informative cues – a situation also known as the communication paradox (Grammer et al., 1997) – could be the main source of emotional arousal in social encounters. Interestingly, research conducted in non-human primates suggests that self-directed activities could be used as reliable behavioural indicators of emotional state associated with social interactions (Aureli & van Schaik, 1991; Aureli, van Schaik, & van Hooff, 1989).

There are a number of ways through which emotional arousal could be linked to social context. First, social tension could result from the uncertainty about the status relationship with the partner. For instance it has been shown that in macaques, uncertainty about the status might give way to increased rates of self-directed activities (Schino, Maestripieri, Scucchi, & Turillazzi, 1990). Second, the perceived risk of aversive consequences might increase the frequency of displacement activities (Rowell & Hinde, 1963; Schino et al., 1990). Social tension could also result from the uncertainty on how to behave next. For example, high rates of scratching were observed in male baboons during group coordination for movement (Kummer, 1968). In addition, Scucchi and colleagues (1991) observed that in opposite-sex pairs of caged long-tailed macaques, males’ displacement activities increased during the periovulatory phase of the female’s menstrual cycle. All in all these studies suggest that various aspects of the social context can lead to a generalized increase in individuals’ arousal, which in turn is reflected in self-directed, or displacement activities.

The relationship between smiling and self-directed activities might depend on the type of smile considered and on the context in which people interact. In general, smiling could lessen arousal because it reduces the ambiguity associated with the social context. This reduction of ambiguity could probably follow the interpretation made by the perceiver of the social situation, through association of a sender’s particular type of smile with some aspect of the context. For example, certain types of smiles could reduce social tension by settling the status relationship between the partners. Interestingly Schino et al. (1990) observed that two unfamiliar macaques caged together showed decreased rates of scratching when formal indicators of status difference – such as the silent bared-teeth display (de Waal & Luttrel, 1985) – were exchanged.

It would be unreasonable to question the role of language in the development of social relationships. However the importance of verbal exchange might be dependent on its link to behaviour, as talking, laughing and smiling are often performed together as parts of a given social episode (Provine & Fischer, 1989). Considering the dynamic flow of social interactions, it has been suggested that laughter regulates conversational behaviour (Dunbar, 1996, p. 191; Seepersand, 1999). For example Provine (1993) showed that the amount of laughter and the relative contribution of speaker and audience laughter depended on the sex composition of a group. For example, in most types of dyads that he surveyed, speakers were laughing more than listeners (see also Vettin & Todt, 2004). Interestingly, that pattern was reversed when the speaker was a man and the audience was composed of women. Overall, male speakers were more efficient at eliciting audience laughter than female speakers (Provine, 1993). Women were also found to laugh more than men when interacting with opposite-sex individuals (Grammer & Eibl-Eibesfeldt, 1990; Mehu & Dunbar, 2008a). We should then expect a relationship between laughter and talking time, and this relationship should depend on the sex of individuals involved.

The relationship between smiling, laughter, listening, and talking could inform about the function of the former two behaviours in social
interactions. For instance smiling and laughter could act as backchannels to send nonverbal feedback to a speaker (Brunner, 1979), in which case they should be positively related to listening time. On the other hand smiling and laughter could be used to emphasize speech, i.e. to draw attention to what is said, or to place positive valence on utterances. In this case we should expect a positive relationship between smiling, laughter and talking time. In addition, the relationship between smiling, laughter and conversation could depend on the type of smiles and laughs considered. Some smile/laugh types could function as backchannels while other types could function as speech emphasizers.

In addition to self-directed activities and conversational behaviour, body contacts are included in the present study in order to provide a measure of intimacy between participants. Physical proximity has been related to smiling and laughter (Chapman, 1975; McAdams, Jackson, & Kirshnit, 1984). If smiling and laughing are involved in the process of bonding between people, they could have a particular relationship to linking behaviours such as non-aggressive body contacts. Frequent and long body contacts observed in informal conversations are believed to reflect closeness between two persons (Argyle, 1988, p. 214; Morris, 1982, p. 140), and such a degree of closeness could be attained with the use of visual or auditory signals sent from a distance. Particular forms of smiling and laughter could therefore play a role in reducing physical space between interacting partners.

The main objective of this article is to investigate the social and behavioural context of different types of smiles and laughs. More specifically, this study investigates how smiling and laughing varies with age and sex of individuals involved in informal, naturally occurring, social interactions; and how these behaviours relate to conversation, body contacts, and displacement activities.

**Method**

**Subjects**

Most subjects were white Caucasians, and due to restriction imposed by anonymity, no systematic examination was made of background variables. Eighty four individuals, 41 men and 43 women, were covertly observed in naturally occurring social interactions in four different bars and cafés. Participants were classified into sex and age classes. Four age classes were defined on the basis of external appearance and approximately corresponded to the following life stages: late teenage (15-25), young adult (25-35), mature adult (35-45), old adult (45 and older). In order to eliminate variation due to group size (Mehu & Dunbar, 2008a), people were observed interacting in dyads. The sex and age of the interacting partner were also recorded.

**Behaviours**

The behaviours recorded in the present study are described in Table 1. Smiles and laughs were classified in different categories. Smiles were classified along two dimensions: spontaneity and mouth opening. The first dimension included two smile types: spontaneous and deliberate. The spontaneous smile was similar to the Duchenne smile described by Ekman and Friesen (1982), i.e. it had to be symmetric and to entail facial activity in the eye region. The deliberate smile category included all other types of smiles, for example "false" or "miserable" smiles (Ekman & Friesen, 1982), and the smiles on which an obvious voluntary control was imposed. The voluntary nature of smiles was inferred using two criteria: symmetry and timing. Asymmetric smiles and smiles with abrupt onsets and offsets were considered as deliberate smiles. The second dimension, mouth opening, also included two categories: open smile and closed smile. The open smile is a smile during teeth
can be observed as a result of mouth opening. It corresponds to Brannigan and Humphries’ (1972) upper smile and broad smile. The closed smile, also called the simple smile (Brannigan & Humphries, 1972) is a smile performed with a closed mouth.

**Table 1. Behavioural Variables**

<table>
<thead>
<tr>
<th>Behaviour</th>
<th>Description</th>
</tr>
</thead>
<tbody>
<tr>
<td>Open Smile</td>
<td>Spontaneous smile open mouth</td>
</tr>
<tr>
<td>Closed Smile</td>
<td>Spontaneous smile closed mouth</td>
</tr>
<tr>
<td>Deliberate</td>
<td>Deliberate smile open mouth</td>
</tr>
<tr>
<td>Open Smile</td>
<td>Deliberate smile open mouth</td>
</tr>
<tr>
<td>Deliberate</td>
<td>Deliberate smile closed mouth</td>
</tr>
<tr>
<td>Closed Smile</td>
<td>Deliberate smile closed mouth</td>
</tr>
<tr>
<td>Low Laughter</td>
<td>Low intensity spontaneous laugh</td>
</tr>
<tr>
<td>Medium</td>
<td>Medium intensity spontaneous laugh</td>
</tr>
<tr>
<td>Laughter</td>
<td>High intensity spontaneous laugh</td>
</tr>
<tr>
<td>High Laughter</td>
<td>High intensity spontaneous laugh</td>
</tr>
<tr>
<td>Deliberate</td>
<td>Deliberate laugh</td>
</tr>
<tr>
<td>Talk</td>
<td>Talking to the partner</td>
</tr>
<tr>
<td>Listen</td>
<td>Listening to the partner</td>
</tr>
<tr>
<td>Out</td>
<td>Attention directed outside the dyad</td>
</tr>
<tr>
<td>Yawn</td>
<td>Yawning</td>
</tr>
<tr>
<td>Nod</td>
<td>Head-nod</td>
</tr>
<tr>
<td>Touch</td>
<td>Brief contact with the partner</td>
</tr>
<tr>
<td>Contact</td>
<td>Long contact with the partner</td>
</tr>
<tr>
<td>Kiss Lip</td>
<td>Kissing partner’s lips</td>
</tr>
<tr>
<td>Kiss Head</td>
<td>Kissing partner’s head</td>
</tr>
<tr>
<td>Kiss Body</td>
<td>Kissing partner’s body</td>
</tr>
<tr>
<td>Auto-Face</td>
<td>Fiddling or self-grooming in the face area</td>
</tr>
<tr>
<td>Auto-Hair</td>
<td>Fiddling or self-grooming one’s hair</td>
</tr>
<tr>
<td>Auto-Hand</td>
<td>Fiddling or self-grooming one’s hands</td>
</tr>
<tr>
<td>Object</td>
<td>Fiddling with an object or with clothes</td>
</tr>
<tr>
<td>Adjust</td>
<td>Adjust one’s hair or clothes</td>
</tr>
</tbody>
</table>

Laughter was categorized according to three levels of intensity: low, medium, and high. The intensity was assessed by the inclusion of four components typical of laughter (Ruch & Ekman, 2001): staccato breathing, vocalization, open-mouth, and body movement (mainly head, shoulders and trunk). The presence or absence of these factors determined the intensity of laughter as follows:

- **Low intensity**: brief exhalations with limited vocalization (up to three notes), mouth slightly open or closed, rhythmic shoulder movements, and the trunk slightly tilted forward or backward.
- **Medium intensity**: prolonged vocalization (more than three notes), open-mouth, same body movement as low intensity but rhythmically more pronounced.
- **High intensity**: loud and prolonged vocalization, open-mouth, head and trunk goes abruptly backward (sometimes forward).

**Procedure**

People were observed from a distance of 5–20m. Individuals were selected if their face was accessible to the observer and if they were interacting in a stable pair, i.e. if no third party came to be involved in the interaction. Interactions with passers-by were not recorded. All occurrences of the behaviours described below were sampled during focal observations performed on one individual at a time (Altmann, 1974). Sampling duration varied from 10 to 30 minutes depending on the availability of individuals ($M = 15.5$, $SD = 4.35$). Data covered a total of 21.7 hours of observation and were collected everyday of the week between 1 and 9 pm, with most observations being made between 4 and 7 pm. Behaviours were encoded in a Psion Workabout 3.1 and then transferred to the

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1 Smiling and laughter rates varied neither with the day of week nor with the time of day that the observations were made.
Observer 5.0 for storage and labelling. The duration of the following behaviours was recorded using the state function of the Observer 5.0: talk, listen, out, and contact. All the other behaviours were described as events.

**Data analysis**

All event behaviours were transformed into a rate per minute by dividing the total frequency by total observation time whereas state behaviours such as talking and listening were converted into percentages of the total observation time. All displacement activities were added together to form a single index (also expressed in rate per minute) representing the general arousal brought about by the social context. Due to the small observed frequency of body contacts between participants, people were classified in two groups according to their involvement in body contacts: contact or no contact.

The effect of age and sex of individuals was assessed using univariate analyses of variance performed separately on each smile type and laughter. Because different forms of smiles could be affected in a different way, each dimension of smiling was the object of a separate analysis. It is important to note that smile dimensions are not exclusive of each other. Therefore the analysis of one category of a dimension involves both categories of the other dimension.

Correlation and regression analyses further investigated the relationships between the different behavioural and contextual variables: the sex and age of the focal individual, the sex and age of the interacting partner, head-nods (rate per min.), self-directed behaviours (rate per min.), laughter (rate per min.), talking and listening time (percentage of the observation period spent talking/listening).

**Results**

**Effect of Sex and Age on Smiling and Laughter**

**Smiling**

The impact of sex composition and age composition of dyads on the different types of smiles was assessed using Student *t* tests. Sex composition of dyads affected the frequency of closed smile rates, *t*(82) = 2.35, *p* < .02. Dyads of the same sex (*M* = 0.73, *SD* = 0.54, *N* = 43) tended to show higher rates of closed smiles than mixed sex dyads (*M* = 0.49, *SD* = 0.39, *N* = 41). Other smile types were not influenced by sex composition of dyads. The age composition of dyads had a marginally significant impact on the frequency of open smiles, *t*(82) = 1.92, *p* < .06, as individuals tended to show more open smiles when interacting with people of their own age (*M* = 0.83, *SD* = 0.73, *N* = 62) than with people of a different age class (*M* = 0.51, *SD* = 0.47, *N* = 22). Other smile types were not affected by the age composition of dyads.

The effects of sex and age on the different types of smiles were further investigated in 2 (sex of focal individual) × 2 (age of focal individual) × 2 (sex of interacting partner) × 2 (age of interacting partner) univariate analyses of variance. A separate analysis was conducted for each type of smile. There was a main effect of age on spontaneous smile rates *F*(1, 83) = 5.34, *p* = .02 and on open smile rates *F*(1, 83) = 5.07, *p* = .03. Individuals younger than 35 years old displayed higher rates of spontaneous smiles and open smiles than older individuals (Table 2).

There was no main effect of age or sex on deliberate smiles. However there was a significant interaction effect between sex and age of interacting partner, *F*(1, 83) = 5.19, *p* = .03, suggesting that the partner’s sex has an influence depending on his/her age. On average, mature men received significantly more deliberate smiles (*M* = 0.22, *SD* = 0.20, *N* = 12) than mature women (*M* = 0.11, *SD* = 0.12, *N* = 12).
= 14), $F(1, 26) = 5.26, p = .03$, whereas young men and women received equal amounts of deliberate smiles, $F(1, 49) = 0.72, p = .40$ (Figure 1). The interaction effect also pointed out that when the interacting partner was a man, mature individuals appeared to received more deliberate smiles ($M = 0.22, SD = 0.20, N = 11$) than younger ones ($M = 0.14, SD = 0.15, N = 32$), $F(1, 35) = 3.73, p = .06$, whereas this effect was non-significant when the partner was a woman, $F(1, 31) = 1.64, p = .21$ (Figure 1).

Univariate analyses also revealed that the frequency of closed smiles was affected by the sex of focal individual, $F(1, 83) = 3.98, p = .05$, men displayed significantly higher rates of closed smiles than women (Table 3). There was also a significant interaction effect between sex of focal and sex of interacting partner on closed smiles, $F(1, 83) = 10.29, p = .002$, indicating that the sex difference was mediated by the sex of the interacting partner. When interacting with other men, men showed significantly higher rates of closed smiles than women, $F(1, 35) = 12.21, p = .001$, whereas this sex difference was absent when the partner was a woman, $F(1, 31) = 1.32, p = .26$. On the other hand, women gave more closed smiles to other women than to men, $F(1, 34) = 24.48, p < .001$. All in all these results indicate that people tend to display more closed smiles to individuals of their own sex (Figure 2).

### Laughter

Laughter of the high intensity category were too rare to be considered for statistical analysis. They were therefore grouped with laughter of medium intensity and treated as a single category of moderate to high intensity laughter. Low intensity laughter constituted a class of its own. The age composition of dyads had a significant impact on the frequency of laughter of high intensities $t(79) = 2.90, p < .005$. Laughs of high intensities were more frequent in same age ($M = 0.19, SD = 0.29, N = 62$) than in mixed age dyads ($M = 0.07, SD = 0.08, N = 22$). Although low intensity laughter was not affected by the age composition nor the sex composition of dyads, younger individuals displayed more of these laughs than older individuals, $F(1, 83) = 4.76, p = .03$ (Table 2). There was no effect of sex or age (of either of the protagonists) on laughter rates.

### Table 2. Frequencies of Smiling by Age Categories

<table>
<thead>
<tr>
<th>Age Of Focal Individual</th>
<th>Young</th>
<th>Mature</th>
<th>Total</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>$N = 57$</td>
<td>$N = 27$</td>
<td>$N = 84$</td>
</tr>
<tr>
<td>Spontaneous Smiles</td>
<td>Mean: 1.37</td>
<td>0.86</td>
<td>1.21</td>
</tr>
<tr>
<td></td>
<td>SD: 0.77</td>
<td>0.73</td>
<td>0.79</td>
</tr>
<tr>
<td>Deliberate Smiles</td>
<td>Mean: 0.15</td>
<td>0.14</td>
<td>0.15</td>
</tr>
<tr>
<td></td>
<td>SD: 0.16</td>
<td>0.13</td>
<td>0.15</td>
</tr>
<tr>
<td>Open Smiles</td>
<td>Mean: 0.90</td>
<td>0.41</td>
<td>0.74</td>
</tr>
<tr>
<td></td>
<td>SD: 0.74</td>
<td>0.42</td>
<td>0.69</td>
</tr>
<tr>
<td>Closed Smiles</td>
<td>Mean: 0.62</td>
<td>0.59</td>
<td>0.61</td>
</tr>
<tr>
<td></td>
<td>SD: 0.49</td>
<td>0.48</td>
<td>0.49</td>
</tr>
<tr>
<td>Low Intensity Laughter</td>
<td>Mean: 0.37</td>
<td>0.18</td>
<td>0.31</td>
</tr>
<tr>
<td></td>
<td>SD: 0.28</td>
<td>0.25</td>
<td>0.28</td>
</tr>
<tr>
<td>High Intensities Laughter</td>
<td>Mean: 0.18</td>
<td>0.12</td>
<td>0.16</td>
</tr>
<tr>
<td></td>
<td>SD: 0.28</td>
<td>0.21</td>
<td>0.26</td>
</tr>
</tbody>
</table>

**Note.** Young adults <35 years, mature adults > 35 years
Table 3. Mean Frequencies (Rate per Minute) and Standard Deviations for Smiling and Laughter Rates According to the Sex Composition of Dyads

<table>
<thead>
<tr>
<th>Sex Of Focal</th>
<th>Male</th>
<th>Female</th>
<th>Total</th>
<th>Male</th>
<th>Female</th>
<th>Total</th>
</tr>
</thead>
<tbody>
<tr>
<td>Sex Of Friend</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>N = 22 N = 19 N = 41</td>
<td>N = 22 N = 21 N = 43</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>spontaneous smiles</td>
<td>Mean 1.38</td>
<td>1.19</td>
<td>1.29</td>
<td>1.00</td>
<td>1.27</td>
<td>1.13</td>
</tr>
<tr>
<td></td>
<td>SD 0.80</td>
<td>1.00</td>
<td>0.89</td>
<td>0.68</td>
<td>0.68</td>
<td>0.68</td>
</tr>
<tr>
<td>deliberate smiles</td>
<td>Mean 0.16</td>
<td>0.14</td>
<td>0.15</td>
<td>0.16</td>
<td>0.14</td>
<td>0.15</td>
</tr>
<tr>
<td></td>
<td>SD 0.13</td>
<td>0.13</td>
<td>0.13</td>
<td>0.20</td>
<td>0.15</td>
<td>0.18</td>
</tr>
<tr>
<td>open smiles</td>
<td>Mean 0.66</td>
<td>0.67</td>
<td>0.67</td>
<td>0.82</td>
<td>0.82</td>
<td>0.82</td>
</tr>
<tr>
<td></td>
<td>SD 0.51</td>
<td>0.93</td>
<td>0.72</td>
<td>0.71</td>
<td>0.61</td>
<td>0.66</td>
</tr>
<tr>
<td>closed smiles</td>
<td>Mean 0.87</td>
<td>0.66</td>
<td>0.77</td>
<td>0.34</td>
<td>0.58</td>
<td>0.46</td>
</tr>
<tr>
<td></td>
<td>SD 0.62</td>
<td>0.44</td>
<td>0.55</td>
<td>0.27</td>
<td>0.41</td>
<td>0.36</td>
</tr>
<tr>
<td>low intensity laughter</td>
<td>Mean 0.35</td>
<td>0.25</td>
<td>0.30</td>
<td>0.28</td>
<td>0.35</td>
<td>0.31</td>
</tr>
<tr>
<td></td>
<td>SD 0.30</td>
<td>0.21</td>
<td>0.26</td>
<td>0.30</td>
<td>0.32</td>
<td>0.31</td>
</tr>
<tr>
<td>high intensities laughter</td>
<td>Mean 0.18</td>
<td>0.10</td>
<td>0.14</td>
<td>0.20</td>
<td>0.16</td>
<td>0.18</td>
</tr>
<tr>
<td></td>
<td>SD 0.29</td>
<td>0.15</td>
<td>0.24</td>
<td>0.34</td>
<td>0.21</td>
<td>0.28</td>
</tr>
</tbody>
</table>

Figure 1. Effect of sex and age of interacting partner on deliberate smiles (young<35years, mature>35years)

Figure 2. Effect of Sex Composition of Dyads on Closed Smiles

Behavioural Context of Smiling and Laughter

Correlation analysis was performed to assess the relationships between the behavioural variables under study (Table 4). Spontaneous smiling was positively associated with open smiles, closed smiles, laughter, and talking time; whereas deliberate smiling was positively related to closed smiles, head nods, listening time, and negatively related to displacement activities. Open and closed smiles were positively associated with laughter rate and
with spontaneous smiles. Due to the small frequencies of body contacts, their relation with smiling and laughter is treated in a separate analysis.

Further analysis was conducted to assess the relative contribution of social and behavioural variables on smiling and laughter. Each type of smile and laugh was treated as a dependent variable in a regression analysis. The different analyses yielded significant models, but the number and type of predictors emerging as significant varied with the type of smile and laugh considered (see Table 5 and 6, respectively).

Spontaneous smile rate was significantly associated with laughter rate, age of focal individual, and talking time. Laughter rate and talking time had a positive relationship to spontaneous smile rate whereas the age of focal was negatively related to spontaneous smiles, indicating that smile rate tended to decrease as age increased. The rate of deliberate smile was positively related to listening time (Figure 3) but not talking time. On the other hand there was a negative relationship between the rate of deliberate smile and the frequency of displacement activities (Figure 4). Open and closed smiles were both significantly and positively related to laughter rate. However these two forms of smiling were affected in a different way by the sex and age of individuals (see above).

The analysis of laughter showed that spontaneous smiling was the most significant predictor and was positively associated with all types of laughter, regardless of intensity (Table 6). In addition, low intensity laughter was positively related to listening time but negatively related to head-nod.

**Smiling, Laughter, and Body Contact**

The overall rate of body contacts did not have the properties needed to perform parametric statistical tests. People were therefore classified in two groups according to their involvement in body contacts (contact or no contact). A Student t-test was conducted to estimate whether these two groups differed with respect to smiling and laughter rates. Men and women were analysed separately.

Analysis showed that the association between smiling and body contacts depended on the type of smile considered and the sex of the individuals involved. There was a significant difference in open smile rates between contact and no-contact individuals in women, \( t(42) = 2.18, p = .03 \), but not in men, \( t(40) = 0.19, p = .85 \), indicating that women who had at least one body contact during the interaction exhibited higher rates of open smiles (\( M = 1.16, SD = 0.61, N = 12 \)) than women who showed no contact (\( M = 0.69, SD = 0.64, N = 31 \)). The sex difference within the ‘contact’ category was also significant, \( t(20) = 2.19, p = .04 \), indicating that women showed higher rates of open smiles (\( M = 1.16, SD = 0.61, N = 12 \)) than men (\( M = 0.71, SD = 0.31, N = 9 \)) when they had at least one physical contact with their friend (Figure 5).

Laughter rates were related to body contacts in a similar way than open smiles were. Women who had at least one physical contact with their friend displayed significantly higher rates of laughter (of any type) (\( M = 0.61, SD = 0.4, N = 12 \)) than women who had no contact (\( M = 0.45, SD = 0.51, N = 31 \)), \( t(42) = 2.83, p = .007 \). However, this was not the case for men \( t(40) = 0.80, p = .43 \). The sex difference within the contact category was marginally significant \( t(20) = 2.02, p = .058 \), suggesting that women who had physical contacts with their friends laughed at higher frequencies (\( M = 0.61, SD = 0.4, N = 12 \)) than men did (\( M = 0.33, SD = 0.19, N = 9 \)) (Figure 6). Men were inclined to laugh more when they had no body contact with their friends than when they had some. This difference, however, was statistically significant for high intensity laughs only, \( t(40) = 2.45, p = .02 \).
Table 4. Correlations between spontaneous smile (sps), deliberate smile (ds), open smile (os), closed smile (cs), laughter (lau), headnods (hn), talking (talk), listening (list), and displacement activities (displ). All variables are expressed in rate per min., except talking and listening time that represented percentage of total observation time spent talking/listening. *p < .05, **p < .01

<table>
<thead>
<tr>
<th></th>
<th>sps</th>
<th>ds</th>
<th>os</th>
<th>cs</th>
<th>lau</th>
<th>hn</th>
<th>talk</th>
<th>list</th>
<th>displ</th>
</tr>
</thead>
<tbody>
<tr>
<td>sps</td>
<td>.02</td>
<td>.80*</td>
<td>.49*</td>
<td>.58**</td>
<td>.08</td>
<td>.22*</td>
<td>.05</td>
<td>.07</td>
<td></td>
</tr>
<tr>
<td>ds</td>
<td>.08</td>
<td>.23*</td>
<td>.47*</td>
<td>.09</td>
<td>.22</td>
<td>.07</td>
<td>.38**</td>
<td>-.25*</td>
<td></td>
</tr>
<tr>
<td>os</td>
<td>-.09</td>
<td>.28*</td>
<td>.14</td>
<td>.06</td>
<td>.09</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>cs</td>
<td>.28*</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>lau</td>
<td>-.04</td>
<td>.09</td>
<td>.17</td>
<td>.07</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>hn</td>
<td>-.17</td>
<td>.57**</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td>-.19</td>
</tr>
<tr>
<td>talk</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td>-.48**</td>
</tr>
<tr>
<td>list</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
</tbody>
</table>

Table 5. Summary of Stepwise Regression Analyses Performed On the Different Types of Smiles (Rates per Minute)

<table>
<thead>
<tr>
<th>Smile type</th>
<th>F</th>
<th>R² adj</th>
<th>Predictors</th>
<th>B</th>
<th>SE B</th>
<th>β</th>
<th>t</th>
</tr>
</thead>
<tbody>
<tr>
<td>Spontaneous</td>
<td>19.02</td>
<td>.39</td>
<td>(constant)</td>
<td>1.80</td>
<td>0.33</td>
<td>5.41**</td>
<td></td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td>laughter</td>
<td>0.27</td>
<td>0.45</td>
<td>.52</td>
<td>5.93**</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td>age foc</td>
<td>-.20</td>
<td>0.08</td>
<td>-.22</td>
<td>-2.55**</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td>talking</td>
<td>0.01</td>
<td>0.01</td>
<td>.18</td>
<td>2.05'</td>
</tr>
<tr>
<td>Deliberate</td>
<td>9.85**</td>
<td>.18</td>
<td>(constant)</td>
<td>0.09</td>
<td>0.05</td>
<td></td>
<td>1.89</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td>listening</td>
<td>0.01</td>
<td>0.01</td>
<td>.37</td>
<td>3.69**</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td>displ.act.</td>
<td>-.04</td>
<td>0.02</td>
<td>-.37</td>
<td>-2.27</td>
</tr>
<tr>
<td>Open</td>
<td>17.72**</td>
<td>.29</td>
<td>(constant)</td>
<td>1.76</td>
<td>0.24</td>
<td></td>
<td>7.23**</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td>laughter</td>
<td>0.18</td>
<td>0.43</td>
<td>.41</td>
<td>4.28**</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td>age foc</td>
<td>-.24</td>
<td>0.75</td>
<td>-.30</td>
<td>-3.13*</td>
</tr>
<tr>
<td>Closed</td>
<td>9.28**</td>
<td>.17</td>
<td>(constant)</td>
<td>0.91</td>
<td>0.08</td>
<td></td>
<td>10.84**</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td>sex foc</td>
<td>-.32</td>
<td>0.10</td>
<td>-.33</td>
<td>-3.30*</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td>laughter</td>
<td>0.09</td>
<td>0.03</td>
<td>.28</td>
<td>2.83*</td>
</tr>
</tbody>
</table>

Notes. Predictors are: sex of focal (sex foc), age of focal (age foc), sex and age of interacting partner, head-nod (rate per min.), laughter (rate per min.), displacement activities (displ. act., rate per min.), talking and listening time (proportion of total observation time). *p < .05, **p < .01, N = 84

Table 6. Summary of Stepwise Regression Analyses on Different Types of Laughter (Rate per Minute)

<table>
<thead>
<tr>
<th>Laughter type</th>
<th>F</th>
<th>R² adj</th>
<th>Predictors</th>
<th>B</th>
<th>SE B</th>
<th>β</th>
<th>t</th>
</tr>
</thead>
<tbody>
<tr>
<td>Low Intensity</td>
<td>17.46**</td>
<td>.39</td>
<td>(constant)</td>
<td>-.11</td>
<td>0.08</td>
<td>-1.33</td>
<td></td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td>spont. smile</td>
<td>0.18</td>
<td>0.03</td>
<td>.50</td>
<td>5.67**</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td>head-nod</td>
<td>-.08</td>
<td>0.02</td>
<td>-.39</td>
<td>-3.71**</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td>listening</td>
<td>0.004</td>
<td>0.00</td>
<td>.23</td>
<td>2.13'</td>
</tr>
<tr>
<td>Medium+High Intensities</td>
<td>16.14**</td>
<td>.15</td>
<td>(constant)</td>
<td>-.002</td>
<td>0.05</td>
<td>-0.04</td>
<td></td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td>spont. smile</td>
<td>0.13</td>
<td>0.03</td>
<td>.40</td>
<td>4.02*</td>
</tr>
</tbody>
</table>

Notes. Predictors are: sex and age of focal individual, sex and age of interacting partner, spontaneous smiles (spont. smile, rate per min.), deliberate smiles (rate per min.), head-nod (rate per min.), displacement activities (rate per min.), talking and listening time (proportion of total observation time). *p < .05, **p < .01, N = 84
Table 7. Logistic Regression Coefficients after Non-Significant Predictors Were Removed from the Model

<table>
<thead>
<tr>
<th></th>
<th>Predictors</th>
<th>B</th>
<th>SE</th>
<th>Wald χ²</th>
<th>p</th>
<th>EXP (B)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Males N = 41</td>
<td>Sex Part</td>
<td>3.49</td>
<td>1.44</td>
<td>5.87</td>
<td>0.01</td>
<td>32.73</td>
</tr>
<tr>
<td></td>
<td>Open Smiles</td>
<td>1.45</td>
<td>0.91</td>
<td>2.55</td>
<td>0.11</td>
<td>4.25</td>
</tr>
<tr>
<td></td>
<td>High Laughs</td>
<td>-11.09</td>
<td>6.06</td>
<td>3.35</td>
<td>0.07</td>
<td>0.00</td>
</tr>
<tr>
<td></td>
<td>Displ. Act.</td>
<td>0.25</td>
<td>0.88</td>
<td>0.08</td>
<td>0.77</td>
<td>1.29</td>
</tr>
<tr>
<td></td>
<td>Forced Smiles</td>
<td>4.11</td>
<td>4.19</td>
<td>0.96</td>
<td>0.33</td>
<td>60.96</td>
</tr>
<tr>
<td></td>
<td>(Constant)</td>
<td>-4.69</td>
<td>2.33</td>
<td>4.07</td>
<td>0.04</td>
<td>0.01</td>
</tr>
<tr>
<td>Females N = 43</td>
<td>Sex Part</td>
<td>-4.13</td>
<td>1.63</td>
<td>6.43</td>
<td>0.01</td>
<td>0.02</td>
</tr>
<tr>
<td></td>
<td>Open Smiles</td>
<td>4.38</td>
<td>1.78</td>
<td>6.07</td>
<td>0.01</td>
<td>79.93</td>
</tr>
<tr>
<td></td>
<td>High Laughs</td>
<td>-0.50</td>
<td>2.27</td>
<td>0.05</td>
<td>0.83</td>
<td>0.61</td>
</tr>
<tr>
<td></td>
<td>Displ. Act.</td>
<td>-1.88</td>
<td>0.97</td>
<td>3.77</td>
<td>0.05</td>
<td>0.15</td>
</tr>
<tr>
<td></td>
<td>Forced Smiles</td>
<td>-11.64</td>
<td>4.83</td>
<td>5.80</td>
<td>0.02</td>
<td>0.00</td>
</tr>
<tr>
<td></td>
<td>(Constant)</td>
<td>0.92</td>
<td>1.32</td>
<td>0.49</td>
<td>0.49</td>
<td>2.52</td>
</tr>
</tbody>
</table>

Notes. The dependent variable is the presence or absence of body contact. Predictors are: age of focal individual, age and sex of interacting partner (sex part), talking and listening time (% of total observation time), and open smiles, deliberate smiles, low and high intensity laughter, and displacement activities (displ. act.), as rates per minute.
Finally, a logistic regression was performed in order to estimate the impact of social context and behavioural variables on the probability to observe at least one physical contact during the interaction. Data were analysed separately for each sex. The model was significant (men: $\chi^2 = 15.21, p = .01$; women: $\chi^2 = 22.82, p < .001; df = 5$), and accounted for between 31% and 48.6% of the variance in men, and between 41.2% and 59.3% of the variance in women. Overall, the accuracy of predictions was 87.8% for males and 81.4% for females. The sex of the partner reliably predicted body contacts in men and women, with a higher probability of having physical contacts when interacting with opposite-sex individuals (Table 7). In addition, open smile rates did reliably predict body contacts in women but not in men. There was also a marginally significant trend suggesting that the amount of moderate to high intensity laughter in men could be negatively associated with the odds of having physical contacts. This was not the case for women’s laughter. Finally, deliberate smiles and displacement activities did predict body contacts in a negative direction in women only, indicating that high rates of deliberate smiles and self-directed behaviours would decrease the probability of having physical contact.

**Discussion**

Functional analyses of behaviour depend on the study of the context in which it occurs and on its consequences for the individuals that display it. The main objective of this article was to investigate the social and behavioural context of smiling and laughter as they naturally occur during dyadic conversations. The present study showed that smiling and laughter rates vary with the age and sex of individuals involved and are connected to conversation, body contact, and displacement activities. These relationships varied with the type of smile and laugh, but also with the social context. The discussion will make sense of these data in terms of how smiling and laughter could contribute to the development of social relationships and lead to social bonding.

**Smiling**

Spontaneous smiling was the only smile type that was invariably associated with laughter rate. The overlap between spontaneous smile and laughter suggests that this form of smile (and to some extent open smile) shares the same motivational basis with laughter. This finding supports previous studies reporting associations between spontaneous smiles and laughter (Mehu & Dunbar, 2008b; Ruch, 1994) and also provides additional evidence that these behaviours frequently co-occur in naturally ongoing interactions. This result also complements a recent perceptual study showing that smiles that are perceived as "amused" more often involve mouth opening, orbicularis oculi activity (cheek raise), and a longer duration (Ambadar et al., 2009). Although these findings seem to contradict the proposal that smiling and laughter have different motivational roots (van Hooff, 1972; Lockard, Fahrenbruch, Smith, & Morgan, 1977), not all smile types were positively associated with laughter (for example deliberate smiles). This indicates that spontaneous and open smiles may have the same motivational basis than laughter whereas deliberate smiles may not.

The reason for the overlap between certain forms of smiling and laughter probably lies behind characteristics of the social context of the interaction (Mehu & Dunbar, 2008b; Preuschoft & van Hooff, 1997). The observation that mature men received considerably more deliberate smiles than young men and mature women implies that deliberate smiles could signal a submissive position, assuming that older men usually enjoy higher social status in modern western societies. In that sense, the deliberate smile may have conserved the
similar appeasing function as the silent bared-teeth display in some macaque species (de Waal & Luttrell, 1985), and the underlying motivation may be quite different from the playful attitude manifested in laughter. This also supports the finding that men displaying non-Duchenne smiles in dyadic interaction are perceived as being more fearful (Merten, 1997). More generally, deliberate smiles could be involved in the communication of friendly, polite, and formal agreement. The association between deliberate smiles and deference is also supported by the observation that this smile type is positively related to listening time. Previous research indeed suggest that the act of speaking is positively related to dominance (Islam & Zyphur, 2005; Mullen, Salas, & Driskell, 1989; Rosa & Mazur, 1979; Schmid-Mast, 2002), indicating that increased rates of deliberate smiles while listening may reflect deference to more assertive and dominant individuals.

Frequencies of deliberate smiles were also negatively correlated with displacement activities, as individuals who displayed high rates of deliberate smiles exhibited fewer self-directed behaviours. This may seem at odds with the proposition that deliberate smiles mostly function in hierarchical contexts, as we would expect these contexts to generate social tension, hence more displacement behaviours. An alternative is that deliberate smiles precisely function to attenuate the social tension induced by hierarchical contexts through the establishment of social status within dyads. This explanation is corroborated by previous research on non-human primates that reported decreased rates of scratching in caged macaques after the display of formal signs of status (Schino et al., 1990). Deliberate smiles could therefore lessen the social tension present in social relationships through a reduction of the ambiguity or uncertainty associated with social status. Previous research showed that smiling is indeed associated with embarrassment and could function as an appeasement display (Goldenthal et al., 1981; Keltner, 1995).

Spontaneous smiling was significantly related to age, with a tendency for younger individuals (< 35 years old) to smile more than older ones. This result replicates the finding of a similar effect of age on spontaneous smiling in group interactions (Adams & Kirkevold, 1978; Mehu & Dunbar, 2008a) and could be explained by a variety of factors. First, younger individuals may have greater needs for cooperative relationships as they have had fewer opportunities than older adults to secure long term resources. The idea that the advertisement of cooperative dispositions could be achieved through spontaneous smiling has received support in other studies (Brown et al., 2003; Mehu et al., 2007), and spontaneous (Duchenne) smiling displayed during an interview has been related to better social integration (Papa & Bonanno, 2008).

Alternatively, younger individuals may smile more because they are, on average, of lower status than older individuals. This explanation, however, can be ruled out because we did not observe any effect of age of interacting partner (a proxy for social status) on spontaneous smiles. Finally, emotional expressivity is known to decrease as people grow older (Carstensen, Gottman, & Levenson, 1995; Gross et al., 1997), and this may also play a role, as a proximal factor, in the negative relationship we observed between age and smiling. The present data should encourage further investigations on the socio-emotional factors involved in the display of smiling across the lifespan.

The sex of individuals also had an impact on smiling. Men showed higher rates of closed smile than women, and this effect was particularly strong when men were conversing with other men. This suggests that closed smiles are crucial to male’s intra-sexual relationships, either in the regulation of status related tensions or in the establishment of male
alliances. Closed smiles usually represent smiles of low intensity or smiles that involve attempts to control or dampen the display. Less expressive smiles are seen in expressions of pride (Mortillaro, Mehu, & Scherer, 2011; Tracy & Robins, 2004), some form of which is motivated by the achievement of social status (Cheng, Tracy, & Henrich, 2010), an aspect is particularly relevant to all-male interactions (Eibl-Eibesfeldt, 1989). Alternatively, lip pressing is often used in smile control and is common in expressions of embarrassment that are also viewed as displays of appeasement (Keltner, 1995). Smiles that are perceived as polite also tend to involve a closed mouth (Ambadar et al., 2009). All in all it is likely that the high rates of closed smiles observed in interactions between men function as regulators of status relationships; either as a way to convey dominance or as a way to appease the partner.

Beside differences in morphological and dynamical aspects, spontaneous and deliberate smiles are believed to differ in meaning, the former being considered as an indicator of positive emotion and the latter as a "social lubricant" (Ekman & Friesen, 1982; Woodzicka & Lafrance 2005, p.140). Deliberate smiles are often called "social smiles" as they are believed to mislead perceivers into thinking that the signaler feels positive when he or she actually intends to mask negative feelings. Although this paper somewhat corroborates the view that different types of smiles have different meanings, the present data suggest that the spontaneous smile is not necessarily less "social" that the deliberate smile, as it may simply have a different social function, possibly bonding through emotional commitment (for a discussion of the role of emotion in social relationships see also Frank, 1988). In so far as possible, future ethological research should include a combination of measures that address both social factors and emotional experience.

Laughter

On the whole, laughter was poorly associated with the social variables under study. Age appeared to be the only factor associated with laughter rates, as younger individuals showed increased rates of laughter than older individuals. This was mostly the case for low intensity laughs. It is not excluded that the negative effect of age on low intensity laughter reflects high rates of nervous laughter in younger individuals. Nonetheless, given the positive association between spontaneous smiles and laughter rates the effect of age on laughter could be described by similar factors (see above). In particular, the idea that laughter and smiling could be involved in bonding or cooperative signalling (Mehu & Dunbar, 2008a, 2008b) was corroborated by the observation that laughter of high intensities mostly occurred between individuals of the same age. The combination of these two findings suggests that laughter could function to cement coalitions (Eibl-Eibesfeldt, 1989, p. 315).

The finding that laughter was not linked to talking gives little support to Provine (1993) who had found that speakers usually laugh more than listeners. On the other hand, laughter of low intensity was positively predicted by listening time, indicating that it could exercise positive feedback on the partner's speech. A similar relationship between laughter and conversation had already been found in a field study showing that pairs of friends continued talking about a given topic for a longer period of time after one of them had laughed than if neither had laughed (Seepersand, 1999). The present data and Seepersand's study both support the idea that laughter acts as a reward that keeps the speaker engaged in verbal interactions (Dunbar, 1996, p. 191; Weisfeld, 1993). Finally, recent research showed that attempts at humour and responses to it work as indicators of interest in the initiation and maintenance of social relationships (Li, Griskevicius, Durante,
Jonason, Pasisz, & Aumer, 2009). Although the present study did not report the verbal content of conversations, it is not excluded that portions of the laughter observed were reactions to humorous comments. Since laughter is also known to occur in response to "unfunny" comments (Provine, 1993), laughter could generally be used by individuals to probe the interaction partner to disclose more information through the verbal channel.

One could argue that the relationship between laughter and listening time can be compared to the association previously observed between deliberate smiles and listening (see above) and that was interpreted as reflecting a possible role of this type of smile in submissive or formal agreement. This interpretation was corroborated by the finding that deliberate smiles were positively associated with head nods. Interestingly, low intensity laughter was positively related to listening but negatively related to head nod (and unrelated to deliberate smiles), indicating that the type of feedback it provides on the partner's talking activity is of a different nature than that provided by deliberate smiles. The interpretation of the relationship between deliberate smiles/laughter and listening time depends on the meaning attributed to head nods. Nodding is typically used as a backchannel in conversations (Brunner, 1979), in particular when people want to ingratiate themselves with the interlocutor, as opposed to when they want to appear competent (Bergsieker, Shelton, & Richeson, 2010; Godfrey, Jones, & Lord, 1986). This suggests that head nods and deliberate smiles are used in the context of deference rather than in self-assertion. Nevertheless, a limitation of this study is that the proportion of deliberate, or "fake", laughter (Ruch & Ekman, 2001) was difficult to assess. It is not excluded that this type of laughter could play a similar role than the deliberate smile in appeasement or deference during tense social situations.

Further research should therefore integrate different types of laughter.

Physical intimacy between partners, as reflected by the presence of body contacts, appeared to be strongly related to women’s, but not men’s, open smiling and laughter. Women who had at least one body contact with their friend exhibited higher rates of laughter and open smiles than females who showed no contact. Furthermore, among individuals who had body contacts, women showed higher rates of laughter and open smiles than men. In fact, open smiles appeared to positively influence the likelihood of having body contacts in women but not in men. Open smiling and laughter might therefore be more important in female’s intimate relationships than in males’, and could, in the former, reflect emotional closeness. The finding that high intensity laughter in men seemed to decrease the odds of having physical contacts with their friend indicate that laughter could have a different function in men and women. Finally, the sex of interacting partner appeared to influence body contacts, as it was more likely to observe such contacts when people interacted with opposite sex individuals. Open smiles and laughter may therefore play a role in female, but not necessarily male, courtship strategies.

A limitation of this study is that it was not possible to evaluate the actual relationship between the members of the dyads. The natural context in which these interactions occurred made it difficult to obtain independent indicators of the nature of social situations. In the absence of such measures, the conclusions made on the role of smiling and laughter in cooperative or hierarchical interactions must be taken cautiously. Another limitation is the lack of information concerning the behaviour of the other individual in the dyad. Behavioural data on both individuals would have allowed for a more precise analysis of the social antecedents and elicitors of smiling and laughter. Such a level of detail is, however, difficult to achieve.
in natural settings because of the cognitive load placed on the observer during live observation, and because the seating arrangements in public places rarely allow an equivalent access to facial expressions of both members of a dyad. Finally, the present results mostly apply to individuals who frequently visit public places such as bars and cafés, and may not necessarily generalize to the entire range of human social interactions. Nevertheless, the present sample covers a larger variety of individuals than is typically considered in psychological research, which mostly involves populations of undergraduate students.

This study provides observational evidence to substantiate earlier claims that different forms of smiles have different "meanings" (Ambadar et al., 2009; Ekman & Friesen, 1982; Keltner, 1995). Observational studies of this sort are helpful because they show the extent to which different forms of smiles are used in everyday interactions. Future research should involve more precise behavioural recording of social interactions taking place in minimally constraining environments, for example by using video recording and automatic image analysis.

All in all, the present study showed that the displays of smiling and laughter vary with the social and behavioural context of interactions. More importantly, the different smile types were not influenced in the same way by context, suggesting that they have different motivational bases and possibly different functions. While spontaneous and open smiles, and to some extent laughter, could function to foster coalitions and intimate bonds between individuals; deliberate and closed smiles may function to regulate more formal aspects of social interactions. These two facets of smiling have in common the inhibition of hostile inclinations in the partner and are comparable to the function(s) of the silent bared-teeth display in other primate species (Preuschoft & van Hooff, 1997; Waller & Dunbar, 2005). The evolution of smiling may therefore reflect a diversification of behavioural strategies that evolved to accommodate the different shades of affiliation that can be expected in complex social groups.

Acknowledgments

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Introduction

While the traditional ethological study of human behavior has long championed analyses of both proximate and ultimate causes of behavior, recent advances in the sciences relevant to these levels of analysis provide fresh ground for interdisciplinary research collaboration, and a need for graduate student training in a new integrative approach to human behavior. Indeed, we believe that we are witnessing a transformation in our conceptual understanding of the interplay between proximate and ultimate factors in the generation of behavior that more and more will require novel thinking about and design of new research strategies concerning the causes of behavior. In this article, we will explore the idea of creating a graduate interdisciplinary program (GIDP) that trains students in the rapidly emerging conceptual advances and methods pertinent to the study of human behavior. We begin by describing what is new about such a GIDP, address why it is needed now, outline its key components, and explore its pros and cons. Finally, we invite your comments on the proposed program.

Marc Méhu, Ph.D., is a postdoctoral researcher at the Swiss Centre for Affective Sciences, University of Geneva. His research interests lie in the study of human social signals, nonverbal behavior and emotional communication. Marc uses a variety of research methods including observational studies and lab experiments, and has also a strong interest in Social Signal Processing, the automatic analysis and synthesis of human behaviour.
anticipate that your constructive commentary will allow us to gauge the appropriateness and desirability of such a program as viewed by a wider international audience.

What’s New?

We believe that the study of the causes of human behavior stands at an exciting new frontier that heralds a not heretofore possible degree and scope of integrating among what is classically known as proximate and ultimate levels of causal explanation. Further, we suggest that this development demands new approaches to graduate training and in turn offers the beneficiaries of this training novel research opportunities that will further a holistic and unified understanding of human behavior. We realize that this is a strong claim about the role of a GIDP in advancing this frontier in the study of human behavior, especially since on the face of it, nothing may appear to be particularly new about bringing these levels of explanation to bear on the study of human behavior. We might well ask, for example, how our proposed endeavor is different from an ethological approach to behavior? After all, the founders of modern ethology (Lorenz, Tinbergen, von Frisch) firmly argued and established the core of an ethological approach to animal behavior as consisting of the combined study of proximate and ultimate causes of behavior (see Hinde, 1982, for a history of the ethological approach). After Tinbergen, these levels of analysis became widely known as the “four causes” of behavior (i.e., proximate causes include immediate and developmental factors, while ultimate causes include adaptive function and phylogenetic derivation).

Our proposal here is that while our GIDP’s approach to human behavior is fully in keeping with the traditional goals of modern ethology, steady advances particularly in evolutionary theory, genetics, epigenetics, neuroscience, and human development now permit a more fully integrated understanding and novel exploration of the points of articulation between proximate and ultimate levels of explanations than was possible earlier. We could say that the emergence of the field of “evo-devo” some years ago heralded this emerging new exploration and understanding of the connection between evolution and development (Raff and Kaufman, 1983; West–Eberhard, 2003; Carroll, 2005). But more recent and continuing aggressive inroads beyond the genome into the epigenome, and the exploration of their evolutionary implications, arguably, have so radically altered the present landscape of our understanding and approach to the evolution and mechanisms of human behavior as to warrant our thinking of it as a new frontier. And given this rapid transformation in our understanding of the causes of behavior, there is now a pressing need for educating our students accordingly.

We cannot here review the many recent advances in the scientific areas just mentioned, but given that these advances and their implications for the study of behavior have gotten much attention in peer-reviewed publications (e.g., see Diamond, 2009; Zhang and Meaney, 2010; Sameroff, 2010) and public media (e.g., Cloud, 2010), we are hopeful that most of the present readership will appreciate the potentially transformative nature of this growing body of research. Nevertheless, we can in broad strokes describe a little more of what we believe is “new” about the field and thus our view of a GIDP. A key advance is in the infusion of evolutionary theory into studies of human development and other proximate mechanisms of behavior. Until very recently, in psychology and other disciplines, the study of human behavioral development has proceeded largely independently of (or uninformed by) evolutionary theory (Moore, 2008, and other papers in same journal issue). One way, for example, in which we might think of our view of the evolution and development of the organism as transformed, is in our understanding of the influence of
“local ecology” on adaptive variation in gene expression and regulation of phenotypic development. Numerous studies on a broad range of species (insects, rodents, human and other primates) have demonstrated the sensitivity of genomic expression (e.g., on/off; up-or-down regulation) and hence phenotypic expression to specific environmental stimuli or features present at various stages of organismic development and even later in adulthood (e.g., Champagne and Mashood, 2009; Cole, 2009). In several studies, the pathways from environmentally-induced modification of gene expression to alterations in neural function to behavior have been carefully defined (e.g., Champagne and Curley, 2005; Meaney, 2010), and surprisingly in some cases these epigenetic mechanisms produce transgenerational behavioral effects (e.g., Champagne, 2008; Curley et al., 2009; Franklin et al., 2010). While not all such environmental influences (e.g., toxins) produce adaptive phenotypic responses, the evolved range of individual adaptive responses or strategies of many organisms, including humans (e.g., see recent model by Ellis et al., 2006 on “orchid” vs. “dandelion” children behavioral strategies), is greater than previously imagined from the standpoint of primarily mutation-regulated phenotypic variation.

This newly discovered range of adaptive plasticity is bringing together researchers from the social-behavioral and biological sciences in new collaborative ventures (e.g., risky adolescent behavior, see Ellis et. al. submitted) offering newly integrative perspectives. Work on adaptive plasticity, for example, is forcing us to reconsider the potential evolutionary significance of variation in individual phenotypes (e.g., adaptive adjustment in individual life history strategies to local social or ecological conditions, see Ellis et al., 2009; 2011), leading to extensions in evolutionary metatheory (e.g., the evolutionary dynamics of populations, evolvability of phenotypes, Lann and Jablonka, 2008). Importantly, the development of global gene assay techniques has overturned the common view that there have been no significant recent evolutionary changes in the human genome (Cochran and Harpending, 2009). Rapid genomic sequencing technology, in turn, has allowed us to move beyond mapping the entire genomes of species to honing in on the regulation of specific regions of DNA that affect neurodevelopment and underlie adaptive phenotypic plasticity. As well, advances in brain imaging technology, is providing detailed insights into the neural substrates of behavior and cognition in real time. This, too, invites new understanding of concepts and methodologies by researchers in diverse disciplines and spawns new research collaborations between social and biological scientists, often posing fundamentally new questions about the mechanisms and evolution of behavior.

At this juncture, it may be helpful to present in a little more detail one set of studies just referred to (summarized in Ellis et al., 2011) in order to illustrate both the advances in the integration of proximate and ultimate causes of behavior and the new fruitful cross-disciplinary collaborations involved. The multi-disciplinary team of investigators shows convincingly how an evolutionary approach brings greater understanding of children’s differential susceptibility to variations in rearing environment in comparison to customary developmental psychopathology models. In the latter traditional clinical framework, children’s susceptibility to environmental stress (e.g., parental neglect) is explained on the basis of (endogenous) characteristics (e.g., of genetic, physiologic, or behavioral origin) that either render them vulnerable or resilient to adverse rearing environments. Environmental adversity does not affect resilient children, however, in vulnerable children it leads to functional impairments or pathology in later life (e.g., depression, high risk-taking). As the authors note, the implicit assumption of this model has
been that vulnerable and resilient children, while clearly responding differentially to adverse environments, would respond similarly to nonadverse or supportive environments, and investigators saw no need to compare resilient and vulnerable children in such favorable environments. However, if from an evolutionary standpoint children’s differential susceptibility to the environment (adverse or nonadverse) is regarded as environmentally-cued distinct adaptive developmental responses (“conditional adaptation”), then we can make sense of the unexpected finding that vulnerable children (the “orchids”) do better in supportive environments than resilient children (the “dandelions”). It turns out that orchid children show heightened sensitivity (mediated by differences in endocrine stress physiology) to both adverse and supportive environments, which leads to their making the best of both harsh and supportive environments. The point here is that traditional developmental psychopathology explanations of susceptibility were not wrong, but their lack of an evolutionary framework restricted the scope of research and made it difficult to incorporate the neuropysiological bases of differential susceptibility. In the end, we have not only a fuller integrated understanding of the proximate and ultimate causes of children’s differential susceptibility, but also different sets of recommendations for ameliorative strategies (e.g., focus on providing supportive environments).

All this is to say, that while all of us have long understood the necessity of bringing multi-level explanations (i.e., proximate/ultimate) to behavior, until relatively recently we had no clear view or example of such integration. This in turn has resulted in scientists from different disciplines, working at different levels of explanation, doing their work in isolation of one another and in the absence of a framework for integrating across levels of analysis. Historically, this has led to considerable conceptual clutter, misunderstanding, and much heated and fruitless debate about the relative importance of environmental versus biological influences on behavior.

This is a well-known history, of course, familiar to us as the pervasive “nature vs. nurture” debate, which has been declared as “dead” many times over. One of us (HDS) recalls the often acrimonious exchanges on this matter between Lehrman and Lorenz, when it frustratingly appeared that both were right in their points of view but neither our state of knowledge nor conceptual understanding seemed to be able to align the two perspectives. On both sides of the debate, few if any believed that genes played no role in behavior or, conversely, that nurture played no role in the expression of behavior. Rather, it seemed to be a “power struggle” between which source was seen as having a greater relative influence on behavior. Hence, ethology (and later sociobiology) unjustifiably became branded as deterministic or reductionistic in its view of behavior, despite the clear recognition by ethologists (including Lorenz) of the contribution of the environment and developmental history to the unfolding of behavior. It seems that for the greater part of the 20th century those studying proximate mechanisms of behavior were little influenced by either ethology or evolutionary biology, and only a handful of social scientists were willing to risk championing an evolutionary (or “zoological”) approach to human behavior, more often than not incurring the wrath of their social science colleagues.

We draw attention to this bit of history because had it been otherwise, we might well more simply be proposing a graduate program in “Human Ethology”. We are, in other words, clearly standing on the broad intellectual shoulders of ethology. But the fact is that the developments in the various sciences we have alluded to have now taken us to a new kind of understanding and integration of the
traditional levels of explanation that “ethology” at the time neither did nor could achieve. As we mentioned before, the founders of human ethology (e.g., Eibl-Eibesfeldt) were strong advocates of integration across levels of explanation, but we suggest that such integration could not be achieved prior to the relatively recent advances in the sciences of genetics, epigenetics, and neuro-behavioral development. As a result, we believe it appropriate to launch a program to signal this emerging new understanding and integration, while in no way disavowing its historical debt and connections to ethology. In a sense, we see the proposed GIDP as the full flowering of human ethology.

**Why Now?**

It strikes us that perhaps for the first time reports of the death of the “nature vs. nurture” debate may not be exaggerated (e.g., see Stotz, 2008). At the risk of over-simplifying, it is now all a matter of working out the two-way pathways from genes to nervous system to behavior and environment, with hypotheses informed by evolutionary theory. The multi-level approach makes no a priori claims about which level is more important in the generation of behavior, nor does it seek to reduce among levels of explanation, but rather it looks toward integration and complementarity among levels of explanation. In this view, and depending on the particular behavior, socio-environmental (proximate) factors, for example, may play as much of a “causal” role in behavior as genes do because evolution sculpted their pathways of causal influence on nervous system function and gene expression. Matt Ridley’s phrase and book title “Nature via Nurture” (2003) well-captures this new interplay among causal factors. We believe that this emerging understanding of the multi-level causes of behavior will usher in a new rapprochement between the social and biological sciences, one that sets aside the old tensions and misunderstandings and provides a fertile ground for interdisciplinary training, research collaborations, and ultimately new applications and career pathways.

One important consequence of the integrative (ethological) approach is that all levels of behavior analysis are cast in an evolutionary framework. In other words, scientists with research interests in proximate causes, for example, in adopting this approach will have their research questions informed by ultimate considerations (evolutionary metatheory, phylogeny). Similarly, scientists working on evolutionary accounts of behavior, must consider the implications of their work for proximate mechanisms. Here, we might note that this neglect has been laid at the door of much of evolutionary psychology, which has largely concentrated on adaptive explanations of human behavior with little thought to how such adaptations might be constrained by or implemented by the underlying biological mechanisms, including developmental ones (Lickliter, 2008). Insofar as an evolutionary framework is foundational to this interdisciplinary approach to the study of behavior, there will have to be wide acceptance across disciplines of the merits of evolutionary theory and methods. While the level of public acceptance of evolution in the US is still embarrassingly low, renewed “outreach” education efforts, such as the recently launched Binghamton University-based undergraduate “Evolutionary Studies (EvoS) Consortium” program (see [http://evostudies.org](http://evostudies.org)), hold promise for changing both public attitudes and receptivity of the wider research community. The EvoS Consortium has grown rapidly since its inception two years ago to now include 41 (mostly) North American colleges and universities, with international membership expected to grow rapidly in the near future. A graduate interdisciplinary program would be well-timed with the expansion of the EvoS Consortium and its gaining of national attention and support from funding agencies. This proposed graduate program would
benefit from the increasing awareness of the broad applicability of evolutionary analysis to human affairs, and the Consortium’s growing resources for teaching and research collaboration. Though this new graduate interdisciplinary program will have a broader training and research mission than EvoS, we would expect significant synergies between the programs, including the incorporation of the EvoS course (“Evolution for Everyone”, or E4E) as a training arena for graduate students (more below).

What are the Key Components?

Envisioning a new GIDP in human behavior requires some thought as to its academic content and related graduate training. First and foremost, such a program will assemble courses drawn from upper division and graduate level courses from participating departments, selected so as to cover the basic theories and methods pertaining to the integrated study of behavior as we have described it. Initial participating departments would include the most obviously relevant, such as Anthropology, Ecology and Evolutionary Biology, Family Studies and Human Development, and Psychology. Content would also be drawn from other departments that offer courses in either methods or applications, such as genetics, or research design and statistics. The second component of such a GIDP is collaborative research. We expect that student advising, research, and dissertation committee membership will involve an appropriate mix of faculty from participating departments. Included in this mix could be an advisor that encourages and assists students in seeking “real world” applications of their research. The third important component that we envision for such a GIDP is professional development for graduate students. As Teaching Assistants, graduate students will receive training in “best practices” or effective teaching to undergraduates from diverse academic backgrounds, including how to evaluate efficacy. These skills can easily be co-opted for public presentations or ‘translation’ of scientific/evolutionary concepts to a lay public. Professional development would also include workshops on effective collaboration, such as interdisciplinary grant writing/seeking, collaborative behavior among colleagues, and new collaborative tools/technology.

A final component to consider is the university culture. As the saying goes, “timing is everything”. In our view, the success of such a GIDP depends on more than intellectual justification, planning, and good will. There must also be already in place evidence of fruitful cross-disciplinary collaboration and ongoing discourse among faculty and students from diverse disciplines, as these are the seedlings from which a GIDP can grow. Either by historical accident or by design, prospects of a GIDP would need a core group of faculty and students with a strong shared interest in the multi-level analysis of human behavior who are willing to or already assemble from several departments at a university —such as Anthropology, Ecology and Evolutionary Biology, Family Studies and Human Development, and Psychology. The particular research interests and professional expertise among these faculty members should cover the full consideration of proximate and ultimate causes of behavior, and most importantly, must be fully oriented toward their integration. Informal cross-disciplinary discussion groups that bring together students and faculty with a shared interest in human behavior are a good way to stimulate interest, encourage collaboration, and gauge the future feasibility of a GIDP.

Many colleges and universities these days are hesitant to implement new programs due to
cost considerations, and so there may be significant administrative hurdles to overcome. One solution may be to launch a GIDP in phases. A phased approach would allow the assessment of the student demand and collaborative climate at the institution, prior to making a large programmatic commitment. During the first phase, one could launch the GIDP as a *minor* that minimally would be available to graduate students in the aforementioned participating departments. For example, a student in Psychology or Family Studies would get a Ph.D. in their “home” department but complete a minor in the GIDP. This mode of implementation will allow for gauging the attractiveness and success of the minor program, with a view toward the eventual creation of a separate, PhD-granting GIDP *major*.

**Pros and Cons**

We strongly believe that the proposed GIDP will contribute to a truly new understanding of the human condition. As such we would like to think that both students would be attracted to such a program and that university administrators would be supportive. However, despite such a worthy potential benefit, we need also to consider some of the potential drawbacks or disadvantages, both from the student perspective, and from the university’s perspective.

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<tr>
<th>Table 1. Student’s Perspective on Enrolling in the Proposed GIDP</th>
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<tr>
<td><strong>Pro</strong></td>
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<tr>
<td>Wide array of training looks good for job seeking in interdisciplinary-oriented institutions</td>
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<tr>
<td>Able to apply for jobs in a variety of disciplines</td>
</tr>
<tr>
<td>Diverse training</td>
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<tr>
<td>Able to communicate evolutionary concepts to all (not just for teaching)</td>
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<tr>
<td>Higher probability of getting a grant (because of collaboration) and funders preferring collaborative projects</td>
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<th>Table 2. University’s Perspective on Supporting the Proposed GIDP</th>
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<tr>
<td><strong>Pro</strong></td>
</tr>
<tr>
<td>Attracts more and better graduate students</td>
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<tr>
<td>Become forefront of interdisciplinary thinking on human behavior</td>
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<tr>
<td>The program can be self-sustaining by utilizing the E4E enrollment income to fund graduate students</td>
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<tr>
<td>Higher probability of getting a grant with overhead (because of collaboration)</td>
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What Do You Think?

Following are some questions about the proposed GIDP to which we seek your responses. These can be answered in two ways: (1) within the context of the Open Peer Commentary process in the Human Ethology Bulletin, or (2) via completing the following online survey, to which a link is posted on www.wildminds.org:

- Do you agree/disagree that the new advances in the scientific study of behavior now open a new arena of cross-disciplinary research (between biological and social sciences)?
- Will a formalized GIDP program serve as a significant stimulus for new interdisciplinary research and funding?
- Will the GIDP graduate look more attractive when job seeking? Will a GIDP graduate be more employable (broad training) or less (diluted/non-traditional) employable in your “home” discipline? Will a GIDP degree be preferable to a standard PhD in one department?
- What name captures the program’s perspective/goals?
- Are there costs/benefits associated with naming the GIDP “Human Ethology”?
- Are there any other benefits or problems of a GIDP that we should consider?

Acknowledgements

We thank our many colleagues at the University of Arizona who have broadened our intellectual horizons and inspired us to put forward the present idea of a GIDP.

References


**Open Peer Commentaries** on this target article may be submitted for publication in the *Human Ethology Bulletin* by any ISHE Member, as per the posted submission policies. For inclusion in the June Issue, all Open Peer Commentaries on the March Target Article must be received by 15 April 2011 to allow sufficient time for peer and editorial review, and any possible revisions that may be required. Authors Responses will be published in the September Issue, and will be due 15 July 2011, for the same reasons. Open Peer Commentaries consist of published, non-anonymous commentaries of up to 1000 words (including references, notes and captions) on peer-reviewed Target Articles, and are solicited from the general readership, and not by special invitation, although commentaries by some selected individuals of special interest might be solicited by the Editor.

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Compiled by Amy Steffes


Current Literature

Compiled by Johan van der Dennen


Gangestad, S. W., Thornhill, R. & Garver-Apgar, C. E. (2010) Men's facial masculinity predicts changes in their female partners' sexual interests across the ovulatory cycle, whereas men's intelligence does not. *Evolution and Human Behavior*, 31, 6, 412-424 (see above)


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Upcoming Conferences and Meetings

Compiled by Amy Steffes

Society for Anthropology of Consciousness
23 – 27 March 2011 – Portland, OR (USA)
www.sacaaa.org/meetings.asp

European Human Behaviour and Evolution Association
24 – 26 March 2011 – Giessen University (Germany)
www.uni-giessen.de/cms/fbz/zentren/philosophie/ehbea2011

Society for Psychological Anthropology
31 March – 3 April 2011 – Santa Monica, CA (USA)
www.aaanet.org/sections/SPA/

Northeastern Evolutionary Psychology Society (NEEPS)
1 – 3 April 2011 – State University of New York at Binghamton (USA)
neepsociety.com/wp-content/uploads/2010/02/neeps-2010-program-pdf/

Constituting the Human
8 – 10 April 2011 – New York City, NY (USA)
macaulay.cuny.edu/conference/constitutingthehuman.html

Society for Interdisciplinary Research on Evolution (SIRE)
12 April 2011 – Fullerton, CA (USA)
psych.fullerton.edu/sire/conference.html

American Association for Physical Anthropology
12–16 April 2011 – Minneapolis, MN (USA)
www.physanth.org/annual-meeting/2011

Wisconsin Symposium on Emotion
13 – 14 April 2011 – Madison, WI (USA)
www.healthemotions.org/symposium/

Society of Human Ecology
20 – 23 April 2011 – Las Vegas, NV (USA)

Association for Psychological Science (APS)
25 – 29 May 2011 – Washington, DC (USA)
www.psychologicalscience.org/index.php/convention

Behavior Genetics Association
5 – 9 June 2011 – Newport, RI (USA)
www.bga.org

Association for Research in Personality
16 – 18 June 2011 – Riverside, CA (USA)
www.personality-arp.org/registration2011.htm

Society for the Study of Evolution
17 – 21 June 2011 – Norman, OK (USA)
www.evolutionsociety.org

Society for Behavioral Neuroendocrinology
24 – 25 June 2011 – Queretaro (Mexico)
www.sbne.org

American Society of Mammalogists
24 – 29 June 2011 – Portland, OR (USA)
www.mammalsociety.org

Human Behavior and Evolution Society
29 June – 3 July 2011 – Montpellier (France)
http://www.hbes2011.univ-montp2.fr/

Summer Institute in Human Ethology
5 – 9 July 2011 – Prague, Czech Republic
www.ishe.org

Animal Behavior Society
25 – 30 July 2011 – Bloomington, IN (USA)
www.animalbehaviorsociety.org

International Ethological Conference
25 – 30 July 2011 – Bloomington, IN (USA)
www.indiana.edu/~beha11

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www.issid2011.com
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