

Social laughter is correlated with an elevated pain threshold

R. I. M. Dunbar^{1,*}, Rebecca Baron³, Anna Frangou⁴,
Eiluned Pearce², Edwin J. C. van Leeuwen⁵, Julie Stow⁶,
Giselle Partridge⁶, Ian MacDonald⁷, Vincent Barra⁶
and Mark van Vugt^{1,5}

¹*British Academy Centenary Research Project, and* ²*Institute of Cognitive and Evolutionary Anthropology, University of Oxford, 64 Banbury Road, Oxford OX2 6PN, UK*

³*Magdalen College, Oxford OX1 4AU, UK*

⁴*Lady Margaret Hall, Oxford OX2 6QA, UK*

⁵*Department of Social and Organizational Psychology, VU University Amsterdam, 57 van der Boechorstraat 1, 1081 BT Amsterdam, The Netherlands*

⁶*School of Biological Sciences, University of Liverpool, Crown Street, Liverpool L69 3BX, UK*

⁷*Department of Biological Sciences, Binghamton University (SUNY), Vestal Parkway East, Binghamton, NY 13902, USA*

Although laughter forms an important part of human non-verbal communication, it has received rather less attention than it deserves in both the experimental and the observational literatures. Relaxed social (Duchenne) laughter is associated with feelings of wellbeing and heightened affect, a proximate explanation for which might be the release of endorphins. We tested this hypothesis in a series of six experimental studies in both the laboratory (watching videos) and naturalistic contexts (watching stage performances), using change in pain threshold as an assay for endorphin release. The results show that pain thresholds are significantly higher after laughter than in the control condition. This pain-tolerance effect is due to laughter itself and not simply due to a change in positive affect. We suggest that laughter, through an endorphin-mediated opiate effect, may play a crucial role in social bonding.

Keywords: laughter; positive affect; pain threshold; endorphins; social bonding

1. INTRODUCTION

Despite the fact that laughter is a human universal that can occur at very high rates under natural conditions and plays an important role in regulating social interaction (including conversation) in humans, it has been little studied [1,2]. While having a number of unique properties, laughter is a feature that we share with the other great apes (in particular, its use in play contexts [3,4]), and this suggests that it has at least as ancient a heritage as any other aspect of our non-verbal behaviour [2]. Not surprisingly, given this lack of attention, the function and evolutionary significance of laughter remains ambiguous. One suggestion has been that laughter conveys signals of social (and especially mating) interest in a companion [5–7]. A more general version of this hypothesis is that laughter induces a positive attitude in the observer, thereby facilitating interaction by reducing threat [7–9]. An alternative is that laughter induces states of positive affect in the laugher, and this facilitates the capacity to learn new things from others (Fredrickson's [10] 'broaden-and-build' hypothesis). Another possibility is that laughter plays a more generalized role in social bonding at the group level [2], thereby facilitating the enhanced prosociality and cooperation that has

played such a crucial role in the evolution of modern humans with their exceptionally large groups [11,12].

None of these explanations, however, provides a plausible *biological* mechanism for how laughter might enhance affect and produce the proposed effects. A tentative answer derives from the fact that humour can have analgesic properties: patients allowed to watch comedy videos required less pain medication than those who watched control videos [13–15]. However, whether patients laughed was never explicitly tested in these experiments. We suggest that it is the physical action of laughing that generates positive affect by triggering activation of the endorphin system. Endorphins are a class of endogenous opioid peptides produced in the central nervous system (CNS) that not only function as neurotransmitters [16] but also play a crucial role in the management of pain through their analgesic properties: β -endorphin, in particular, appears to play a critical role in buffering the organism against the effects of physiological and psychological stress [17–24]. More importantly, in the present context, endorphins are also thought to play a central role in social bonding, especially in primates [25–27].

Because CNS endorphins do not cross the blood–brain barrier [28,29], it has been common practice to assay endorphin levels using pain threshold [20,22,30–34]. This assay assumes that high levels of CNS endorphins will be associated with an elevated pain threshold. Using pain thresholds as a proxy for endorphin release, we

* Author for correspondence (robin.dunbar@anthro.ox.ac.uk).

Electronic supplementary material is available at <http://dx.doi.org/10.1098/rspb.2011.1373> or via <http://rspb.royalsocietypublishing.org>.

report a set of six experiments that test the hypothesis that, compared with a control condition, laughter elevates endorphin titres.

2. METHODS

Because pain thresholds vary between individuals, we used a within-subjects comparison: subjects took a pain threshold test, undertook an experimental or control task and then repeated the pain assay. In five experimental studies, the task involved watching either a comedy video or a non-humorous factual documentary. In a sixth study, we sampled actors and audiences at live performances under completely naturalistic conditions. Details of the videos and selection of subjects are given in the electronic supplementary material.

(a) *Experiments 1–3*

Experiments 1–3 use different experimental designs to confirm the main effect of laughter on pain threshold. Because humans do not laugh readily when watching even the funniest performances alone [1,35] and laughter is 30 times more likely to occur in social contexts than when alone [36], all subjects were tested in groups.

In experiment 1, 15 females and 20 males were tested in groups of 2–6 in a between-subjects design, with half acting as the experimental group (watching a comedy video) and half as the control group (watching a factual documentary). Experiment 2 used a within-subjects design to confirm that subjects responded differentially to comedy and neutral videos when tested on both. In this experiment, 10 females and six males were tested in five groups of 3–4 individuals in a within-subject design with each subject acting as their own control (each group was tested twice, first in the control condition and then in the experimental condition). In experiment 3, three males and two females (mean age = 23.2 years, range 22–24) formed the experimental group, and eight males and three females (mean age = 24.6 years, range = 20–32) the control group.

Pain tolerance was assayed using a frozen vacuum wine cooler sleeve (frozen to -16°C for the start of each trial; maximum duration 180 s) in experiments 1 and 2, and a mercurial sphygmomanometer (inflated to a maximum pressure of 260–280 mmHg) in experiment 3. In each case, subjects were asked to indicate when they could no longer stand the pain (see electronic supplementary material).

In experiments 1 and 2, we estimated how much time participants spent laughing while watching videos by scan sampling each participant at 15 s intervals, recording whether or not they were laughing.

(b) *Experiments 4 and 5*

In experiments 1–3, all subjects were tested in groups, making it difficult to determine whether the change in pain threshold was due to some kind of group effect rather than to laughter. Experiment 4 tested for this confound by separating out the two effects. In this experiment, 21 males (mean age = 25.7 ± 9.4 years, range 18–55) and 41 females (mean age = 24.0 ± 8.7 s.d. years, range 18–58) were randomly assigned to one of three conditions in which they watched either a neutral video alone, a comedy video alone or a comedy video in a group of four (each of 15 min duration). Laughter was recorded on individual dictaphones hung from each subject's neck, and subsequently scan-sampled for the presence/absence of laughter at 15 s intervals.

Owing to equipment malfunction, laughter data are available only for 58 subjects and pain threshold data for 60.

A second possible confound relates to the interface between affect and endorphins. Although endorphins are known to mediate affect [21], the change in pain threshold might be due to changes in affect rather than the laughter itself. Experiment 5 separated out these two effects. In this experiment, 14 males (mean age = 23.0 years, range 18–32) and 36 females (mean age = 19.9 years, range 18–27) were randomly assigned to watch one of the three 15 min video clips (neutral, positive affect and comedy). Participants in the neutral condition either watched the film alone in a small cubicle ($n = 10$) or in single-sex groups of four ($n = 8$). Those in the affect and comedy conditions watched the videos only in single sex groups of four. Participants were audio-recorded with a hidden microphone. The absolute number of laughter bouts for the group as a whole was scored from the audio recordings without differentiating who was laughing.

In both experiments, pain tolerance was assessed following the procedure used in experiment 3. Subjects completed a positive and negative affect scale (PANAS) [37] before and after watching the video to measure the change in positive and negative affect.

(c) *Experiment 6*

In order to determine whether the results of experiments 1–3 generalized to the real world outside the laboratory, we used live theatrical performances at the Edinburgh Fringe Festival in August 2008 as an outdoor laboratory. In this experiment, 27 performers and technical crew members (10 females, 17 males: mean age = 21.6 years, range 18–30) participated in this experiment over a period of 18 days. Several of these appeared as both actor and audience on different days (depending on whether they were performing), yielding a total of 41 cases in all. Four experimental conditions were created: *comedy actors* (six female, 11 male), *comedy audience* (six female, 11 male), *drama actors* (one female, three male) and *drama audience* (one female, two male).

In each condition, participants were required to complete a pain test at least an hour before performing or watching the show and to repeat this immediately after the show. Because experiment 6 was conducted outside the laboratory, we used a standard ski exercise as a pain assay: subjects lean against a wall with their legs at right angles (as if sitting on a straight-backed chair) until it becomes too painful and they collapse onto the ground [38,39]. Subjects completed a questionnaire self-reporting how much they had laughed during the performance (on a 0–5 scale).

Because individual subjects were sampled at several performances (mean 2.9, range 1–6) in any given condition, all analyses are based on mean values for individual subjects in each condition. However, to determine whether there was any habituation effect, we correlated difference in the time for which the position was held with order of performance for all subjects who had three or more trials. Of the 11 subjects who met this criterion, six exhibited positive correlations and five negative correlations, suggesting that there was no consistent bias owing to multiple trials (binomial test: n.s.).

(d) *Statistical analysis*

Change in pain threshold was normally distributed in all but one of 16 conditions across the six experiments, and overall, does not differ from a normal distribution (Fisher's

meta-analysis: $\chi^2 = 24.76$, d.f. = $2 \times k = 32$, $p = 0.857$; see electronic supplementary material). Percentage of time spent laughing was significantly different from a normal distribution, but ln-transforms of (%laugh + 1) (to remove 0 values) was not; so ln-transformed data are used for analysis in this case. All statistical tests are two-tailed except in respect of the variable *condition*: as a directional hypothesis is being tested in this case (comedy > neutral), a one-tailed test is appropriate.

3. RESULTS

(a) Laughter rates

To establish that laughter rates differ across experimental and control conditions in the way predicted, we first tested for an effect of video type on laughter rates in the three experiments where laughter by individual subjects was sampled by scan-sampling (experiments 1, 2 and 4). Subjects spent significantly more time laughing in the comedy condition than in the control condition (electronic supplementary material, figure S1). Condition (video type) is the only factor that significantly affects the dependent variable (study: $F_{1,115} = 1.31$, $p = 0.275$; condition: $F_{3,115} = 166.92$, $p < 0.001$; gender: $F_{1,115} = 1.69$, $p = 0.196$; condition \times gender: $F_{3,115} = 0.36$, $p = 0.670$). Scheffé *post hoc* tests confirm that laughter rates (i) are significantly higher in all the comedy conditions than in all the control conditions, (ii) are significantly higher in the comedy-alone condition than in the control conditions, (iii) are significantly higher in all the group comedy conditions than in the comedy-alone condition (all at $p < 0.001$), and (iv) do not differ significantly between the experimental (comedy) conditions across experiments ($p > 0.600$).

(b) Laughter and pain tolerance

Figure 1 plots the difference in pain tolerance before and after viewing the video for the control (neutral) versus the experimental (comedy) groups for experiments 1–3. Condition is the only factor that has a significant effect, with change in pain tolerance being significantly higher in experimental (comedy video) conditions than in control (neutral video) conditions (condition: $F_{1,77} = 4.09$, $p = 0.024$; study: $F_{2,77} = 1.01$, $p = 0.370$; gender: $F_{2,77} = 3.91$, $p = 0.051$; condition \times gender: $F_{1,77} = 1.15$, $p = 0.287$). Note that there is a marginally significant effect of gender ($p = 0.051$). This effect is not, however, consistent across experiments: in the experimental condition, females showed a stronger effect than males in experiments 1 and 2, but the reverse was the case in experiment 3.

The critical test for the endorphin hypothesis is that there should be a significantly elevated pain threshold in the experimental conditions, but no change ($\delta = 0$) in the control conditions. We tested this by comparing the distribution of pain threshold differences (after minus before) in a one-sample *t*-test against the null hypothesis that $\delta = 0$. Taken together, change in pain threshold is significantly greater than zero in the three experimental conditions (experiment 1: $t_{16} = 2.12$, $p = 0.007$; experiment 2: $t_{15} = 1.12$, $p = 0.140$; experiment 3: $t_4 = 9.46$, $p < 0.001$; Fisher's meta-analysis: $\chi^2 = 30.44$, d.f. = 6, $p < 0.00001$), but not significantly greater than zero in the three control conditions (experiment 1: $t_{17} = 1.50$,

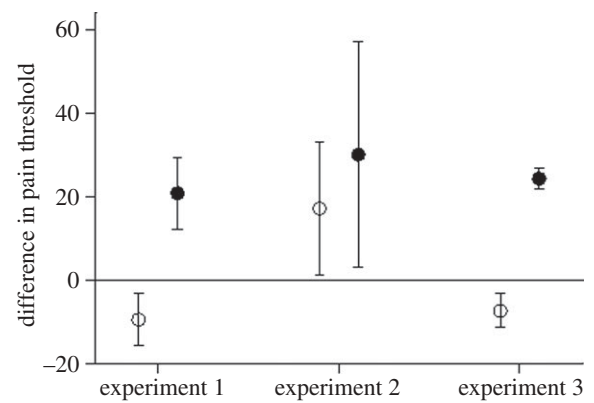


Figure 1. Experiments 1–3: mean (\pm s.e.) difference in pain threshold (post-test minus pre-test) under the two conditions (control: neutral video, open symbols; experimental: comedy video, solid symbols). Experiments 1 and 3 were between-subjects designs; experiment 2 was a within-subjects design. Pain threshold was indexed using a frozen wine cooler sleeve (experiments 1 and 2) or a sphygmomanometer (experiment 3). Experiment 3 demonstrates that alternative indices of pain threshold yield similar results. Sample sizes (left to right): 18, 17, 16, 16, 11, 5.

$p = 0.924$; experiment 2: $t_{15} = 1.09$, $p = 0.146$; experiment 3: $t_{10} = 1.79$, $p = 0.948$; Fisher's meta-analysis: $\chi^2 = 6.91$, d.f. = 6, $p = 0.329$).

(c) Group and affect confounds

In experiment 4, we checked whether the elevated pain thresholds in the comedy condition were due simply to being tested in a group or whether there is a parametric effect of the amount of laughter. Ln-transformed laughter rates varied significantly across conditions (electronic supplementary material, figure S1; $F_{2,55} = 94.29$, $p < 0.001$), with all differences between conditions being significant (group comedy > comedy alone > neutral alone: Scheffé *post hoc* tests, $p < 0.001$). Positive affect scores did not differ significantly between conditions, although they were in the same direction ($F_{2,59} = 2.96$, $p = 0.060$). Condition has a significant effect on pain threshold (figure 2; $F_{2,56} = 5.56$, $p = 0.007$), but gender does not ($F_{1,56} = 0.97$, $p = 0.318$); there is a significant condition \times gender interaction ($F_{1,56} = 5.33$, $p = 0.008$), but this may reflect the rather small sample size for males in the group comedy condition. Scheffé *post hoc* tests for condition indicate that threshold changes in the neutral-alone condition are significantly smaller than that in the group comedy ($p = 0.043$), but the comedy-alone condition does not differ significantly from either the neutral-alone condition ($p = 0.861$) or the group comedy condition ($p = 0.110$), indicating that laughter exhibits something closer to a dose–response effect than a step change due solely to a group effect: experiencing comedy in a group ramps up the laughter response, and this is reflected in a proportional change in pain threshold.

Experiment 5 sought to determine whether the change in pain threshold is due to laughter or to affect alone. It did this by asking subjects to view a non-humorous positive affect video, as well as the usual neutral and comedy videos. Ln-transformed laughter rates varied significantly across conditions ($F_{3,46} = 46.64$, $p < 0.001$), with all differences between conditions being significant (comedy group >

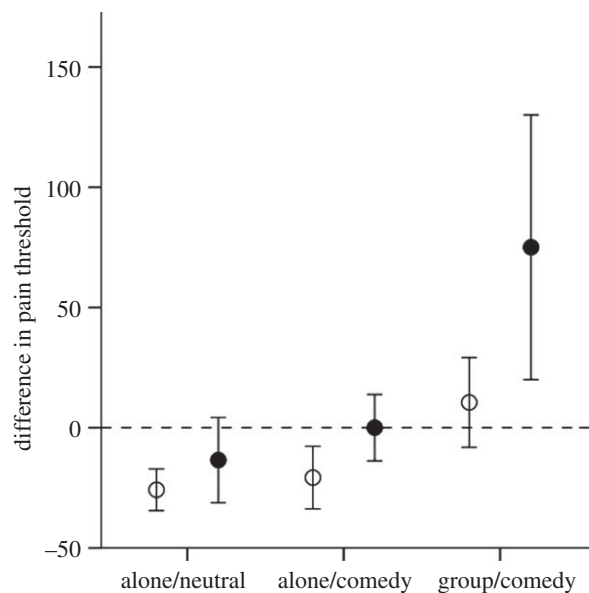


Figure 2. Experiment 4: mean (\pm s.e.) change in pain threshold (post-test minus pre-test) for females (open symbols) and males (solid symbols) under three different conditions: neutral video watched alone, comedy video watched alone and comedy video in groups of four. Pain threshold was indexed using a sphygmomanometer. Sample sizes (left to right): 18, 8, 17, 7, 8, 2.

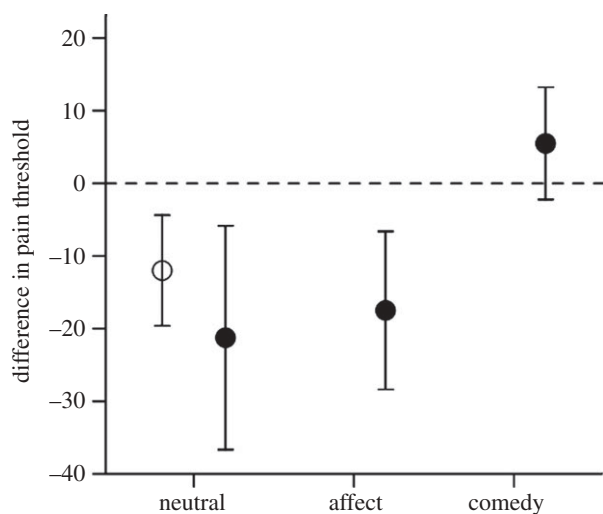


Figure 3. Experiment 5: mean (\pm s.e.) change in pain threshold (post-test minus pre-test) under three conditions (neutral video, positive affect-only video and comedy video) for subjects who watched the video alone (open symbols) or in groups of four (solid symbols). Pain threshold was indexed using a sphygmomanometer. Sample sizes (left to right): 10, 8, 12, 20.

neutral group > affect group > neutral alone: Scheffé *post hoc* tests, $p \leq 0.031$). Positive PANAS scores showed a broadly similar pattern across conditions ($F_{3,46} = 3.54$, $p = 0.022$), but only the scores in the group comedy condition were significantly ($p = 0.022$) higher than those in the other three conditions (which did not themselves differ: $p \geq 0.198$). The differences in mean pain threshold across the four conditions are shown in figure 3. We first tested whether pain thresholds in the positive affect condition are significantly different from those in the two neutral conditions (they are not: $F_{2,27} = 0.16$, $p = 0.856$),

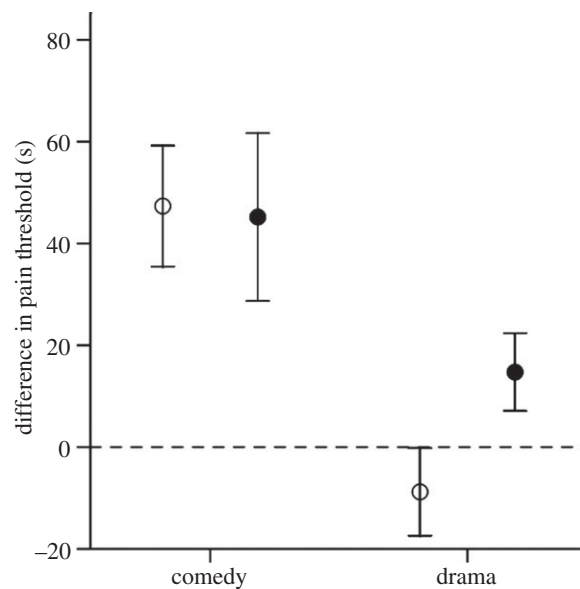


Figure 4. Experiment 6: mean (\pm s.e.) difference in pain threshold (post-test minus pre-test) for actors (open symbols) and audience (solid symbols) in live theatre performances of stand-up comedy versus drama (no laughter condition). Pain threshold indexed using the Madsen *et al.* [38] skiing task and the measure is the time for which the position was held (in seconds). Sample sizes (left to right): 17, 17, 4, 3.

and then whether pain thresholds in the group comedy condition are significantly greater than the neutral and affect conditions combined (they are: $F_{1,48} = 4.95$, $p = 0.016$ one-tailed). Thus, laughter can be differentiated from positive affect *per se* in its effect on pain threshold, even though laughter may enhance (or be correlated with) enhanced positive affect.

(d) *Laughter under natural conditions (experiment 6)*

As a final test of the hypothesis, we ran a version of the experiment under natural conditions at live theatrical performances. Mean self-report laughter scores in the comedy condition were 3.5 ± 0.87 for actors and 3.38 ± 1.12 for audience members (modal value = 4 for both, on a Likert scale of 1–5), indicating that both performers and audience actively laughed during the sampled sessions. Subjects in the drama events did not laugh at all (all scores = 0). Figure 4 plots the change in pain threshold separately for actors and audience in the comedy and drama events. There was a significant effect of condition (comedy versus drama: $F_{1,38} = 3.86$, $p = 0.022$ one-tailed), but no effect owing to status (actor versus audience: $F_{1,38} = 0.16$, $p = 0.901$). More importantly, the difference in pain threshold is significantly greater than $\delta = 0$ for both actors ($t_{16} = 3.983$, $p < 0.001$) and audience ($t_{16} = 2.742$, $p = 0.007$) in the comedy events, but not in the drama events (though sample sizes are small in the latter; actors: $t_3 = -1.022$, $p = 0.618$; audience: $t_2 = 1.932$, $p = 0.193$; all tests one-tailed).

4. DISCUSSION

We tested the hypothesis that social laughter elevates pain thresholds both in the laboratory and under naturalistic

conditions. In both cases, the results confirmed that when laughter is elicited, pain thresholds are significantly increased, whereas when subjects watched something that does not naturally elicit laughter, pain thresholds do not change (and are often lower). These results can best be explained by the action of endorphins released by laughter.

An important distinction is drawn between Duchenne laughter (relaxed, unforced laughter that is stimulus-driven and emotionally valent, involving involuntary contraction of the *orbicularis oculi* muscles) and non-Duchenne laughter (context-driven and emotionless, with no *orbicularis oculi* involvement) [1,2,40,41]. Neuroimaging evidence suggests that these two types of laughter involve different neural pathways [42]. The involuntary nature of Duchenne laughter is largely responsible for the well-known contagion effect whereby we are stimulated to laugh just by others laughing. Precisely because Duchenne laughter is intensely social and contagious [1,40], it is likely that the endorphin effect is limited to this form of laughter. Indeed, only Duchenne laughter has the capacity to mitigate negative emotions and stress [40].

Most of the phenomena that trigger endorphin release involve physical exercise (running, circuit-training, rowing, etc. [18,33,43–45]) or other forms of pressure on the body surface (e.g. grooming and massage [46]). In the case of laughter, we assume that the functional mechanism is the muscular exertion involved in sustained laughter. As the sonograms in Davila Ross *et al.* [4] illustrate, ape laughter typically consists of a series of alternating exhalations and inhalations, whereas that of humans typically consists of a sustained series of exhalations without drawing breath (see also [1]). (This capacity to maintain a long series of exhalations is crucial to speech [1,47,48].) It is this long series of exhalations that appears to be exhausting (hence triggering endorphin release), and this might be either because the physical effort involved is itself significant or because emptying the lungs in an uninterrupted series of exhalations is taxing.

Although it has been argued that positive affect plays an important role in the bonding of groups of individuals [49], experiment 5 suggests that affect alone may be insufficient to create a significant endorphin surge. Given that neuroimaging studies have demonstrated a direct relationship between endorphin uptake at receptor sites and perceptions of affect [21], our results suggest that the sense of heightened affect in this context probably derives from the way laughter triggers endorphin uptake.

Although laughter plays an important role in regulating conversation in humans [1], it may also play a significant role in facilitating social bonding among groups of individuals [2,11,12,50]. In both primates and humans, for example, laughter plays an important signalling role during social play [1–3]. The capacity to sustain laughter for periods of several minutes at a time may exaggerate the opioid effects, thus ramping up the sense of heightened affect that humans experience in these contexts. A key aspect of this may be that social (or Duchenne) laughter is highly socially synchronized [1]. In a study of physical exercise (rowing), synchronized activity ramped up endorphin production (as indexed by change in pain threshold) by a factor of two over that generated by exercise alone [33]. If the opiate effects of endorphins create a sense of wellbeing, synchronized activity might then lead to

enhanced prosociality, and hence group bonding and cooperation [50]. Indeed, even simple behavioural synchrony is sufficient to enhance cooperative behaviour in subjects [51]. As we might anticipate a similar effect arising from social laughter, a promising future development would be to test whether sustained laughter in groups enhances prosociality or altruistic behaviour.

Laughter contrasts with many more conventional aspects of non-verbal communication in one important respect: it seems to create euphoric states in the performer similar to those experienced in communal music-making, dancing and some of the rituals of religion [52]. There is some evidence to suggest that these euphoric states are also associated with the release of endorphins [11,53]. Singing, dancing and rituals have long been recognized as important components in the process of bonding whole communities in traditional societies, a process referred to variously in the anthropological literature as ‘effervescence’ [54] and ‘communitas’ [55]. An obvious hypothesis is that all these activities exploit the same psychopharmacological mechanism (the release of endorphins) as social grooming does in primates [25,26], and so provide a bridging mechanism (i.e. a form of grooming at a distance) that enables humans to bond social communities that are much larger than those that primates can bond by social grooming alone [12–25,56]. This possibility awaits detailed testing.

This research was supported by the British Academy Centenary Research Project.

REFERENCES

- 1 Provine, R. 1996 *Laughter: a scientific investigation*. London, UK: Faber & Faber.
- 2 Gervais, M. & Wilson, D. S. 2005 The evolution and functions of laughter and humor: a synthetic approach. *Q. Rev. Biol.* **80**, 395–430. (doi:10.1086/498281)
- 3 Waller, B. & Dunbar, R. I. M. 2005 Differential behavioural effects of ‘smiling’ and ‘laughing’ in chimpanzees (*Pan troglodytes*). *Ethology* **111**, 129–142. (doi:10.1111/j.1439-0310.2004.01045.x)
- 4 Davila Ross, M., Owren, M. J. & Zimmermann, E. 2009 Reconstructing the evolution of laughter in great apes and humans. *Curr. Biol.* **19**, 1–6. (doi:10.1016/j.cub.2009.05.028)
- 5 Grammer, K. 1990 Strangers meet: laughter and non-verbal signals of interest in opposite sex encounters. *J. Nonverbal Behav.* **14**, 209–236. (doi:10.1007/BF00989317)
- 6 Grammer, K. & Eibl-Eibesfeldt, I. 1990 The ritualization of laughter. In *Natürlichkeit der sprache und der kultur: acta colloquii* (ed. W. Koch), pp. 192–214. Bochum, Germany: Brockmeyer.
- 7 Owren, M. J. & Bachorowski, A. 2003 Reconsidering the evolution of non-linguistic communication: the case of laughter. *J. Nonverbal Behav.* **27**, 183–200. (doi:10.1023/A:1025394015198)
- 8 Bachorowski, J.-A. & Owren, M. J. 2001 Not all laughs are alike: voiced but not unvoiced laughter readily elicits positive affect. *Psychol. Sci.* **12**, 252–257. (doi:10.1111/1467-9280.00346)
- 9 Li, N. P., Griskevicius, V., Durante, K. M., Jonason, P. K., Pasisz, D. J. & Aumer, K. 2009 An evolutionary perspective on humor: sexual selection or interest indication? *Pers. Soc. Psychol. Bull.* **35**, 923. (doi:10.1177/0146167209334786)

- 10 Fredrickson, B. L. 2004 The broaden-and-build theory of positive emotions. *Phil. Trans. R. Soc. Lond. B* **359**, 1367–1377. (doi:10.1098/rstb.2004.1512)
- 11 Dunbar, R. I. M. 2008 Mind the gap: or why humans aren't just great apes. *Proc. Br. Acad.* **154**, 403–423.
- 12 Dunbar, R. I. M. 2009 Mind the bonding gap: constraints on the evolution of hominin societies. In *Pattern and process in cultural evolution* (ed. S. Shennan), pp. 223–234. San Francisco, CA: University of California Press.
- 13 Cogan, R., Cogan, D., Waltz, W. & McCue, M. 1987 Effects of laughter and relaxation on discomfort thresholds. *J. Behav. Med.* **10**, 139–144. (doi:10.1007/BF00846422)
- 14 Zillman, D., Rockwell, S., Schweitzer, K. & Sundar, S. 1993 Does humor facilitate coping with physical discomfort? *Motiv. Emot.* **17**, 1–21. (doi:10.1007/BF00995204)
- 15 Rotton, J. & Shats, M. 1996 Effects of state humor, expectancies, and choice on postsurgical mood and self-medication: a field experiment. *J. Appl. Soc. Psychol.* **26**, 1775–1794. (doi:10.1111/j.1559-1816.1996.tb00097.x)
- 16 Bloom, F. E. 1983 The endorphins: a growing family of pharmacologically pertinent peptides. *Annu. Rev. Pharmacol. Toxicol.* **23**, 151–170. (doi:10.1146/annurev.pa.23.040183.001055)
- 17 Akil, H., Madden, J., Patrick, R. L. & Barchas, J. D. 1976 Stress-induced increase in endogenous opiate peptides: concurrent analgesia and its partial reversal by naloxone. In *Opiate and endogenous opiate peptides* (ed. H. W. Kosterlitz), pp. 63–70. Amsterdam, The Netherlands: Elsevier.
- 18 Harbach, H., Hell, K., Gramsch, C., Katz, N., Hempelmann, G. & Teschemacher, H. 2000 β -endorphin (1-31) in the plasma of male volunteers undergoing physical exercise. *Psychoneuroendocrinology* **25**, 551–562. (doi:10.1016/S0306-4530(00)00009-3)
- 19 Basbaum, A. I. & Fields, H. L. 1984 Endogenous pain control systems: brainstem spinal pathways and endorphin circuitry. *Annu. Rev. Neurosci.* **7**, 309–338. (doi:10.1146/annurev.ne.07.030184.001521)
- 20 Mueller, C. *et al.* 2010 Basal opioid receptor binding is associated with differences in sensory perception in healthy human subjects: a [18 F]diprenorphine PET study. *NeuroImage* **49**, 731–737. (doi:10.1016/j.neuroimage.2009.08.033)
- 21 Zubieta, J.-K., Smith, Y.-R., Bueller, J. A., Xu, K., Kilbourn, M. R., Jewett, D. M., Meyer, C. R., Koeppe, R. A. & Stohler, C. S. 2001 Regional μ -opioid receptor regulation of sensory and affective dimensions of pain. *Science* **293**, 311–315. (doi:10.1126/science.1060952)
- 22 Zubieta, J.-K., Smith, Y. R., Bueller, J. A., Xu, Y., Kilbourn, M. R., Jewett, D. M., Meyer, C. R., Koeppe, R. A. & Stohler, C. S. 2002 μ -opioid receptor-mediated antinociception differs in men and women. *J. Neurosci.* **22**, 5100–5107.
- 23 Zubieta, J.-K., Ketter, T. A., Bueller, J. A., Xu, Y., Kilbourn, M. R., Young, E. A. & Koeppe, R. A. 2003 Regulation of human affective responses by anterior cingulate and limbic μ -opioid neurotransmission. *Arch. Gen. Psychiatry* **60**, 1145–1153. (doi:10.1001/archpsyc.60.11.1145)
- 24 Bodnar, R. J. & Klein, G. E. 2006 Endogenous opiates and behavior: 2005. *Peptides* **27**, 3391–3478. (doi:10.1016/j.peptides.2006.07.011)
- 25 Curley, J. P. & Keverne, E. B. 2005 Genes, brains and mammalian social bonds. *Trend Ecol. Evol.* **20**, 561–567. (doi:10.1016/j.tree.2005.05.018)
- 26 Dunbar, R. I. M. 2010 The social role of touch in humans and primates: behavioural function and neurobiological mechanisms. *Neurosci. Biobehav. Rev.* **34**, 260–268. (doi:10.1016/j.neubiorev.2008.07.001)
- 27 Machin, A. & Dunbar, R. I. M. In press. The brain opioid theory of social attachment: a review of the evidence. *Behaviour*.
- 28 Kalin, N. H. & Loewinger, B. L. 1983 The central and peripheral opioid peptides: their relationships and functions. *Psychiatr. Clin. N Am.* **6**, 415–428.
- 29 Boecker, H., Sprenger, T., Spilker, M. E., Henriksen, G., Koppenhoeffler, M., Wagner, K. J., Valet, M., Berthele, A. & Tolle, T. R. 2008 The runners' high: opioidergic mechanisms in the human brain. *Cereb. Cortex* **18**, 2523–2531. (doi:10.1093/cercor/bhn013)
- 30 Young, R. F., Bach, F. W., van Norman, A. S. & Laksh, T. L. 1993 Release of β -endorphin and methionine-enkephalin into cerebrospinal fluid during deep brain stimulation for chronic pain. *J. Neurosurg.* **79**, 816–825. (doi:10.3171/jns.1993.79.6.0816)
- 31 Zubieta, J.-K., Heitzeg, M. M., Smith, Y. R., Bueller, J. A., Xu, K., Koeppe, R. A., Stohler, C. S. & Goldman, D. 2011 COMT val¹⁵⁸met genotype affects μ -opioid neurotransmitter responses to a pain stressor. *Science* **299**, 1240–1243. (doi:10.1126/science.1078546)
- 32 Depue, R. A. & Morrone-Strupinsky, J. V. 2005 A neuro-behavioral model of affiliative bonding: implications for conceptualizing a human trait of affiliation. *Behav. Brain Sci.* **28**, 313–395.
- 33 Cohen, E., Ejsmond-Frey, R., Knight, N. & Dunbar, R. I. M. 2010 Rovers' high: behavioural synchrony is correlated with elevated pain thresholds. *Biol. Lett.* **6**, 106–108. (doi:10.1098/rsbl.2009.0670)
- 34 Master, S. L., Eisenberger, N. I., Taylor, S. E., Naliboff, B. D., Shirinyan, D. & Lieberman, M. D. 2009 A picture's worth: partner photographs reduce experimentally induced pain. *Psychol. Sci.* **20**, 1316–1318. (doi:10.1111/j.1467-9280.2009.02444.x)
- 35 Freedman, J. L. & Perlick, D. 1979 Rowing, contagion and laughter. *J. Exp. Soc. Psychol.* **15**, 295–303. (doi:10.1016/0022-1031(79)90040-4)
- 36 Provine, R. R. & Fischer, K. R. 1989 Laughing, smiling, and talking: relation to sleeping and social context in humans. *Ethology* **83**, 295–305. (doi:10.1111/j.1439-0310.1989.tb00536.x)
- 37 Watson, D. & Clark, L. A. 1994 The PANAS-X. Manual for the positive and negative affect schedule: expanded form. University of Iowa, Iowa City, IA, USA. See <http://www.psychology.uiowa.edu/Faculty/Clark/PANAS-X.pdf>.
- 38 Madsen, E., Tunney, R., Fieldman, G., Plotkin, H., Dunbar, R., Richardson, J. & McFarland, D. 2007 Kinship and altruism: a cross-cultural experimental study. *Br. J. Psychol.* **98**, 339–359. (doi:10.1348/000712606X129213)
- 39 Harrison, F., Sciberras, J. & James, R. 2011 Strength of social tie predicts cooperative investment in a human social network. *PLoS ONE* **6**, e18338. (doi:10.1371/journal.pone.0018338)
- 40 Keltner, D. & Bonanno, G. A. 1997 A study of laughter and dissociation: distinct correlates of laughter and smiling during bereavement. *J. Pers. Soc. Psychol.* **73**, 687–702. (doi:10.1037/0022-3514.73.4.687)
- 41 Vettin, J. & Todt, D. 2004 Laughter in conversation: features of occurrence and acoustic structure. *J. Nonverbal Behav.* **28**, 93–115. (doi:10.1023/B:JONB.0000023654.73558.72)
- 42 Iwase, M. *et al.* 2002 Neural substrates of human facial expression of pleasant emotion induced by comic films: a PET study. *NeuroImage* **17**, 758–768. (doi:10.1006/nimg.2002.1225)
- 43 Colt, E. W. D., Wardlaw, S. L. & Frantz, A. G. 1981 The effects of running on plasma β -endorphin. *Life Sci.* **28**, 1637–1640. (doi:10.1016/0024-3205(81)90319-2)
- 44 Gambert, S. R., Hagen, T. C., Garthwaite, T. L., Duthie, E. H. & McCarthy, D. J. 1981 Exercise and the

- endogenous opioids. *N Engl. J. Med.* **305**, 1590–1591. (doi:10.1056/NEJM198112243052619)
- 45 Howlett, T. A., Tomlin, S., Ngahfoong, L., Rees, L. H., Bullen, B. A., Skrinar, G. S. & MacArthur, J. W. 1984 Release of β -endorphin and met-enkephalin during exercise in normal women in response to training. *Br. Med. J.* **288**, 295–307. (doi:10.1136/bmj.288.6435.1950)
- 46 Keverne, E. B., Martensz, N. & Tuite, B. 1989 Beta-endorphin concentrations in cerebrospinal fluid of monkeys are influenced by grooming relationships. *Psychoneuroendocrinology* **14**, 155–161. (doi:10.1016/0306-4530(89)90065-6)
- 47 Aiello, L. C. 1996 Terrestriality, bipedalism and the origin of language. In *Evolution of culture and language in primates and humans* (eds J. Maynard Smith, G. Runciman & R. I. M. Dunbar), pp. 269–289. Oxford, UK: Oxford University Press.
- 48 MacLarnon, A. & Hewitt, G. 1999 The evolution of human speech: the role of enhanced breathing control. *Am. J. Phys. Anthropol.* **109**, 341–363. (doi:10.1002/(SICI)1096-8644(199907)109:3<341::AID-AJPA5>3.0.CO;2-2)
- 49 Spoor, J. R. & Kelly, J. R. 2004 The evolutionary significance of affect in groups: communication and group bonding. *Group Proc. Intergr. Relations* **7**, 398–412. (doi:10.1177/1368430204046145)
- 50 Lakin, J. L., Jefferis, V. E., Cheng, C. M. & Chartrand, T. L. 2003 The chameleon effect as social glue: evidence for the evolutionary significance of nonconscious mimicry. *J. Nonverbal Behav.* **27**, 145–162. (doi:10.1023/A:1025389814290)
- 51 Wiltermuth, S. S. & Heath, C. 2009 Synchrony and cooperation. *Psychol. Sci.* **20**, 1–5. (doi:10.1111/j.1467-9280.2008.02253.x)
- 52 Ehrenreich, B. 2006 *Dancing in the streets*. New York, NY: Metropolitan.
- 53 Birk, L. S., Tan, S. A., Fry, W. F., Napier, B. J., Lee, J. W., Hubbard, R. W., Lewis, J. E. & Eby, W. C. 1989 Neuroendocrine and stress hormone changes during mirthful laughter. *Am. J. Med. Sci.* **298**, 390–396. (doi:10.1097/00000441-198912000-00006)
- 54 Durkheim, E. 1965 *The elementary forms of religious life*. New York, NY: Free Press.
- 55 Turner, V. 1966 *The ritual process: structure and anti-structure*. Ithaca, NY: Cornell University Press.
- 56 Lehmann, J., Korstjens, A. H. & Dunbar, R. I. M. 2007 Group size, grooming and social cohesion in primates. *Anim. Behav.* **74**, 1617–1629. (doi:10.1016/j.anbehav.2006.10.025)