

Exorcising Grice's ghost: an empirical approach to studying intentional communication in animals

Simon W. Townsend^{1,2}, Sonja E. Koski^{3,4}, Richard W. Byrne⁵, Katie E. Slocombe⁶, Balthasar Bickel⁷, Markus Böckle⁸, Ines Braga Goncalves¹, Judith M. Burkart³, Tom Flower⁹, Florence Gaunet¹⁰, Hans Johann Glock¹¹, Thibaud Gruber¹², David A.W.A.M. Jansen¹, Katja Liebal¹³, Angelika Linke¹⁴, Adam Miklosi¹⁵, Richard Moore¹⁶, Carel P. van Schaik³, Sabine Stoll⁷, Alex Vail¹⁷, Bridget Waller¹⁸, Markus Wild¹⁹, Klaus Zuberbühler¹² & Marta B. Manser¹

1 Institute of Evolutionary Biology and Environmental Studies, University of Zurich, Zurich, 2 Department of Psychology, University of Warwick, Coventry, 3 Anthropology Institute and Museum, University of Zurich, Zurich, 4 Centre of Excellence in Intersubjectivity in Interaction, University of Helsinki, 5 School of Psychology and Neuroscience, St Andrews University, St Andrews, 6 School of Psychology, University of York, York, 7 Department of Comparative Linguistics, University of Zurich, Zurich, 8 Department for Psychotherapy and Biopsychosocial Health, Danube University, Krems, 9 Percy Fitzpatrick Institute, University of Cape Town, Cape Town, 10 Laboratoire de Psychologie Cognitive, Aix-Marseille University/CNRS, Marseille, 11 Institute of Philosophy, University of Zurich, Zurich, 12 Cognitive Biology, University of Neuchatel, Neuchatel, 13 Department of Education and Psychology, Free University of Berlin, Berlin, 14 German Seminar, University of Zurich, Zurich, 15 Department of Ethology, Eötvös Loránd University, Budapest, 16 Berlin School of Mind and Brain, Humboldt-Universität zu Berlin, 17 Zoology Department, University of Cambridge, Cambridge, 18 Department of Psychology, Portsmouth University, Portsmouth, 19 Philosophy Seminar, Basel University, Basel

Keywords: communication, language evolution, intentionality, vocalisation, gesture

17 ABSTRACT

18

19 Language's intentional nature has been highlighted as a crucial feature distinguishing it from other
20 communication systems. Specifically, language is often thought to depend on highly structured
21 intentional action and mutual mind-reading by a communicator and recipient. Whilst similar abilities
22 in animals can shed light on the evolution of intentionality, they remain challenging to detect
23 unambiguously. We revisit animal intentional communication and suggest progress in identifying
24 analogous capacities has been complicated by (i) the assumption that intentional (that is, voluntary)
25 production of communicative acts requires mental-state attribution, and (ii) variation in approaches
26 investigating communication across sensory modalities. To move forward, we argue a framework
27 fusing research across modalities and species is required. We structure intentional communication into
28 a series of requirements, each of which can be operationalised, investigated empirically, and must be
29 met for purposive, intentionally communicative acts to be demonstrated. Our unified approach helps
30 elucidate the distribution of animal intentional communication and subsequently serves to better
31 clarify what is meant by attributions of intentional communication in animals and humans.

32 Contents

33 I Introduction

34 II The new framework

35 1) An example of intentionality in vocal communication assessed with the proposed criteria

36 III Conclusion

37 IV References

38

39 I. Language is considered to be one of the pinnacles of human biological evolution (Fitch 2010). Its
40 emergence in the *Homo* lineage was presumably enabled by the presence of a set of cognitive abilities
41 and ecological conditions not shared by other species. One candidate for these abilities is the capacity
42 to act with, and understand, communicative intentions. The philosopher of language, Paul Grice (1957,
43 1982), was pivotal in highlighting the importance of such a psychological framework for
44 communication and many authors working in the ‘Gricean’ tradition have followed him in arguing
45 that the ability for intentional communication requires a sophisticated, pre-existing, metapsychological
46 framework in which speaker and hearer (or signaler and receiver) mutually understand one another’s
47 intentions and beliefs (Sperber & Wilson 1995, Sperber 2000, Tomasello 2008, Scott-Phillips 2015a).

48

49 Within Grice’s influential analysis of speaker meaning there exist three clauses (Strawson 1964, Jacob
50 1997), the conjunction of which form the basis for Grice’s theory of communication. For a signaler, S,
51 to mean something via utterance x requires that: i) S intends that S’s utterance of x induce a response, r ,
52 in receiver, R; ii) S intends that R recognises that S has intention (i), and iii) S intends that R’s
53 recognition of S’ intention functions at least partly in the motivation for R’s response, r . On this
54 account, we not only intend to influence the receiver (through the production of a stimulus) when
55 communicating, we also want them to recognise that we are acting with such intentions, and respond
56 on the basis of recognising this. In linguistic pragmatics this communication of intention (surmised by
57 these three clauses) is often referred to as ostensive or Gricean communication and the reiterated
58 mutual perspective taking that underlies this process has consequently been highlighted as a defining
59 feature of human linguistic communication (e.g. Grice 1982, Dennett 1983, Sperber and Wilson 1995,
60 Sperber 2000, Tomasello 2008, Scott-Phillips 2015a).

61

62

63 Given the proposed centrality of Gricean characterisations of communication (Grice 1957) to human
64 communicative interaction, questions have been raised as to the uniqueness of these aspects of human
65 language. The extent to which human and non-human animal communication could involve the same
66 underlying psychological framework has been debated (Gomez 1994, Tomasello 2008, Scott-Phillips
67 2015a, b, Moore 2015a). One reason for this is that on standard accounts (Dennett 1983, Sperber
68 2000), Gricean communication requires that communicators are capable of entertaining very complex
69 metarepresentations – that is, representations of others’ mental states. Dennett (1983, 1988) played a
70 critical role in initial attempts to operationalise animals as intentional systems by differentiating
71 between various orders of the metarepresentational complexity that intentional communication
72 requires, based on Grice’s analysis (Dennett 1983). Zero-order intentionality attributes no mentality or
73 intention to the communicative signalling of animals. First-order intentionality requires that the
74 signaler intends to signal to produce a response in the recipient, but does not require that the recipient
75 recognise this. Second-order intentionality involves complementing the intention to signal with the
76 attribution of mental states (by the recipient to the signaler); whilst third- order intentionality requires
77 that the signaler intend for the recipient to attribute to her the intention to signal. Finally, fourth-order
78 intentionality requires that signaler and recipient, alike, represent both the signaler’s goal and her
79 intention that the recipient recognise that goal (Dennett 1983, Sperber and Wilson 1995, Scott-Phillips
80 2015a,b).

81

82 Although this operationalisation would appear to serve as a useful guide to identifying what type of
83 intentionality an animal communicative system displays, it has also generated problems related to
84 what the levels of intentionality represent. As Dennett has noted, both first and higher orders of
85 intentionality require that an act of signalling is produced voluntarily and in a goal-directed way.
86 However, second order intentionality (and beyond) likely employs cognitive mechanisms of a
87 qualitatively different kind - since it requires that both signaler and recipient engage in some form of

88 mental state attribution. For this reason, second order intentionality has received most interest because
89 it has been generally considered as more “human” or, as Grice highlighted, as more indicative of “true”
90 linguistic communication (Grice 1957) and hence a step further along the continuum towards human
91 language (Scott-Phillips 2015a). One major consequence is that it has since become common-place to
92 assume that in order to demonstrate convincing evidence that animal vocal production is intentional
93 and thus relevant to human language, at the very least, an attribution of mental states during vocal
94 communication is required.

95
96 This emphasis of mental state attribution is unhelpful for two reasons. Firstly, whilst adult humans are
97 competent at reiterated mental-state attribution, there is evidence that younger children find high
98 orders of metarepresentation difficult (Wimmer & Perner 1983, Liddle & Nettle 2006). Some working
99 in primate cognition have therefore argued that, if standard interpretations of Grice are right, then
100 Gricean communication would be too difficult for both animals and human children. If this is correct,
101 then standard interpretations must overstate the cognitive pre-requisites of Gricean communication
102 (Gomez 1994, Moore 2014, 2015a,b) – and human and animal communication may share a common
103 psychological framework after all. The less-intellectualised approaches to human communication are
104 supported by the argument that even in adults, speech production and interpretation seems not to
105 always require inference computation or belief ascription about speaker intentions (Millikan 1984).
106 Furthermore, experimental studies under controlled conditions have repeatedly demonstrated that
107 mind-reading is not deployed automatically during social and communicative situations (Keysar et al.
108 2003, Apperly et al. 2006) and is even sometimes impeded by the surrounding social environment
109 (McClung et al. 2013).

110
111 A second reason for resisting the mental state attribution approach is that it risks obscuring the goals
112 of comparative psychology and biology. The comparative approach does not aim to show that animals
113 communicate in a way that fully equates to human communication; instead it aims to elucidate

114 evolutionary precursors of crucial components of human language (Seyfarth et al. 1980, Zuberbühler
115 2005). The comparative study of semantics, for example, does not hinge on the discovery of symbolic
116 conventions, displaced in time and space from the referents of communicative behaviour (Tomasello
117 2008). In that case, to try to evaluate what other animals are doing by human standards is to risk
118 failing to do justice to their abilities. A more theory-neutral approach to studying intentional
119 communication would therefore be better.

120

121 In line with this idea, over the last ten years Byrne, Hopkins, Leavens, Tomasello, and colleagues have
122 taken a less theory-laden approach to intentionality. This approach sidesteps the requirement that
123 intentional communication involves understanding the minds of others and does not assume that
124 intentional use of communicative signals involves the sorts of ‘ostensive-inferential’ communication
125 that thinkers in the Gricean tradition have argued characterises human communication. Through
126 borrowing behavioural markers implemented by developmental psychologists to distinguish between
127 reflexive and more intentional gestural communication in children (Bates et al. 1979), progress has
128 been made in identifying traits that are precursors to distinctively human intentional communication
129 systems (Leavens et al. 2005, Liebal et al. 2006). In a similar way to humans, non-human primates,
130 primarily great apes, also communicate with each other by gesturing. Observations of the production
131 of gestures suggest that they fulfil a number of the criteria specified for intentionality in
132 communicative signals (table 1). Individuals have, for example, been observed to take into account the
133 attention state of the receiver, only gesturing when selected receivers are appropriately attentive
134 (Leavens et al. 2005), and to elaborate or change signal if their initial signal fails to reach the apparent
135 goal (Cartmill and Byrne 2007). By avoiding the question of mental state attribution, and by focusing
136 on behavioural markers of flexible and goal-directed communication, an array of studies have
137 demonstrated first order intentionality in the communication of our closest living relatives (Call &
138 Tomasello 2007, Pika & Liebal 2012, Byrne 2016).

139

140 However, there exists some variation in the criteria of intentionality that individual studies apply to
141 gestural signals and rarely has there been an attempt to apply all criteria to a single signal in a study
142 species (but see Leavens et al. 2004). Moreover, each individual marker of intentionality in isolation
143 can be explained through lower-level mechanisms, without needing to invoke intentionality. For
144 example, sensitivity to the attention state of the receiver could simply be a learned discrimination
145 where signals are only produced when a receiver's face can be seen; persistence of a signal may have
146 nothing to do with an intention to communicate with an as yet unresponsive receiver, but simply that
147 signal production is emotionally driven and only when the goal is met does the underlying emotion
148 change and terminate signal production (Liebal et al., 2013, Gaunet & Massiou 2014, Savalli et al.
149 2014). Therefore, it is important, before invoking first order intentionality, to demonstrate convergent
150 evidence from a number of markers of intentionality for the same signal and species (Liebal et al.
151 2013, though see Vail et al. 2013). Although multiple cases of converging evidence do not amount to a
152 proof, the probability of a behaviouristic explanation decreases.

153

154 Whilst gestural studies highlight potential phylogenetic precursors to the intentional communication
155 of humans and provide crucial comparative data, similar evidence from vocal communication studies
156 has not been considered as equally convincing. Despite numerous attempts, researchers have failed to
157 teach enculturated apes to produce spoken language (Yerkes and Yerkes 1929, Hayes 1951). As their
158 vocalisations are commonly produced in specific contexts, it has been traditionally assumed that
159 vocalisations are the product of low level emotional processes and are best characterised as
160 involuntary responses to specific stimuli rather than voluntary, goal-directed signals (Dennett 1983,
161 Notman & Rendall 2005, Tomasello 2008). Furthermore, invasive procedures have shown that call
162 initiation in monkeys is mediated by limbic rather than cortical structures in the brain (Jurgens 1992).
163 On the other hand, some studies suggest that vocal and non-vocal sounds are used intentionally.

164 Leavens, Hopkins and colleagues have shown that great apes use voiced and unvoiced sounds in a
165 controlled manner that implies flexibility and intentionality (Russell et al. 2005, Hopkins et al 2007,
166 Hostetter et al. 2007, Hopkins et al. 2011). More recent studies, under natural conditions, have
167 provided additional support for intentionality in ape vocalisations (Crockford et al. 2012, 2015, Schel
168 et al. 2013). Moreover, multiple studies have shown vocalisations to be dependent on the surrounding
169 social audience in a variety of species (Marler et al. 1986, Zuberbühler 2008, Crockford et al. 2012).
170 These so called “audience effects” are not solely due to simple, arousal mediated, social facilitation
171 effects (Zajonc 1965), as might be the case when examining the presence or absence of conspecifics
172 (Tomasello 2008). Instead, they incorporate more subtle social and behavioural variations, e.g.
173 relationship quality (Slocombe et al. 2010, Mazinni et al. 2013, Schel et al. 2013,) or response of
174 receivers (Wich and de Vries 2006).

175
176 Despite this body of data, the existence of intentional vocal communication in animals is still disputed
177 (Tomasello 2008). Given the central role intentionality plays in human language and the apparent
178 disparity between the intentional production of gestures and non-intentional vocalisations in non-
179 human primates, it has been argued that language must have evolved via a gestural, rather than a vocal,
180 route (Corballis 2002, Tomasello 2008). This theoretical reasoning certainly adds fuel to the fiery
181 debate surrounding language’s evolutionary emergence. But unfortunately it fails to consider the fact
182 that the researchers working with gestures and vocalisations, respectively, are operating from different
183 bases (Slocombe et al. 2011). Animal vocal communication researchers are investigating how the
184 production of vocalisations may or may not be used to influence the mental states of receivers, often
185 with negative results (Rendall et al. 2000; but see Crockford et al. 2012, Schel et al. 2013). By contrast,
186 gestural communication researchers are using an in-place suite of behaviours, derived from child
187 developmental work, to address how goal-directed and hence intentional (Dennett’s first order
188 intentionality) gestural production is, predominantly in primates. This means that the research into

189 vocalisations tacitly employs a more demanding criterion for intentionality than the research into
190 gestures. As a result, comparing intentional production of animal signals at different levels in the two
191 different modalities commits the mistake of not comparing like with like, and hence renders it difficult
192 to draw reliable conclusions about differences in intentionality across these modalities.

193

194 To resolve these conceptual and methodological difficulties we propose to ‘level the playing field’
195 with an updated framework in which the intentional nature of animal communication, irrespective of
196 modality, can be operationalised and systematically assessed. A single framework approach will
197 facilitate direct comparative work amongst species and communicative mediums, providing a more
198 holistic picture of the evolution of human intentional communication.

199

200 II. *The new framework*

201 The framework that we propose consists of three distinct criteria, each of which needs to be met by a
202 signal type before intentionality is ascribed to it. We do not abandon consideration of cognitive
203 components to intentionality, but instead argue that questions about whether or not vocal
204 communication is produced voluntarily and in a goal-directed way can be answered independently of
205 questions about whether signaler and receiver are engaged in mind-reading. Therefore, we return to
206 goal-directedness and its role in intentional behaviour as the first criterion requiring satisfaction.

207

208 Animal **S** intentionally communicates **I** to receiver **R** if the following three propositions all hold:

209

210 1) *S acts with a goal with the content I*

211 Goal directed behaviour has been a central focus of comparative psychology research over the last
212 three decades. At a more rudimentary level the notion of goal-direction involves the role of motor-
213 processes organising action towards physical targets (Kenward et al. 2009). However, goal-

214 directedness has also been implicated in intentional behaviour, as opposed to automatic or habitual
215 behaviour (Heyes and Dickinson 1990). Here it is necessary to show that the goal-directed behaviour
216 is based upon knowledge of the relationship that exists between the action and its consequences (Wit &
217 Dickinson 2009). Hence within our new framework we shift the cognitive emphasis to demonstrating
218 that communication is goal-directed.

219
220 Whilst we appreciate that operationalisation of goal-directedness is not straightforward, it is a far more
221 tangible and relevant criterion than the demonstration of mental state attribution. Previous studies
222 probing the intentionality of primate gestures have emphasised the role of persistence and elaboration
223 in identifying goal-directedness. In line with this, we argue that goal-directedness can be empirically
224 investigated more generally by merging these criteria with the identification and application of
225 ‘stopping rules’ (Burkart et al. 2015). When a signaler possesses a goal for its communication, it
226 would stop upon reaching the goal, but persist and/or elaborate the signal when the goal is not reached
227 (Leavens et al. 2005). Thus, as with any other behavioural data, regular and reliable observations
228 fulfilling the criteria (e.g. a goal-dependent cessation of communication, or indeed persistence and
229 elaboration in the absence of the goal being met) are critical to demonstrating the presence of a goal,
230 causally linked with the signal. Furthermore, experimental manipulation of goal end states leading to
231 premature or delayed goal accomplishment is an additional, complementary way, to assess the causal
232 link between the goal and the communicative signal.

233

234 *2) S produces voluntary, recipient directed signals as a means to reach the represented goal*

235 We agree with Leavens et al. (2004) and Moore (2015b) that to show intentionality, behaviour must be
236 under volitional control and recipient-directed. Criteria generated from studies of intentional
237 communication in infants (Bates et al. 1979) represent a valuable set of measures to address these
238 conditions (see table 1). One indicator of voluntary control is selective use of the signal, and in

239 particular, selectively producing or withholding a signal in response to social factors such as audience
240 composition and behaviour (social use). As we highlighted above, social context could in principle be
241 part of a complex stimulus to which an automatic, innate signal production mechanism responds. Thus
242 Hurford (2007, page 232) argues that only if ‘circumstances under which calls are given are too
243 implausibly complex to be hardwired into the genes’ should we infer these signals are voluntary.
244 Indicators of the recipient-directed nature of a signal include social use, audience checking and
245 sensitivity to attentional state (Ristau 1991, Povinelli et al. 2003, Liebal et al. 2004, Leavens et al.
246 2005, Schel et al. 2013). Every signal type and study species is different. So, whilst it has been
247 suggested that the more criteria satisfied the greater the confidence that a signal is indeed intentional
248 (Schel et al. 2013), this may not always be plausible (e.g. certain criteria apply only to the visual
249 domain). Thus we would argue for a strict *a priori* selection procedure of criteria to ensure fair
250 comparisons across species and modalities.

251

252 3) *S's signaling behaviour changes the behaviour of R in ways conducive to realising I*

253 As the last condition for intentionality, we focus on the behaviour of the receiver with respect to the
254 signal produced. Given our shift of focus away from signaler or receiver mental state attribution we
255 only require that the communicative behaviour of the signaler elicits a change in the behaviour of the
256 receiver. To rule out the pitfall of simply treating any behavioural change in the receiver as sufficient
257 for intentionality, we strengthen our condition by specifying that the change in the receiver's
258 behaviour must be repeatable, consistent and in line with the apparent intentions of the signaler.

259 In order to demonstrate how our conditions can be operationalised, we shall now interpret data from a
260 recent study on the alarm calling behaviour of chimpanzees within the new framework and assess its
261 intentionality.

262

263 **An example of intentionality in vocal communication assessed with the proposed criteria**

264 In a similar way to many primate and non-primate species, chimpanzees (*Pan troglodytes*
265 *schweinfurthii*) produce vocalisations when faced with dangerous situations (e.g. python or leopard
266 presence, inter-group interactions). However, due to the rare occurrence of such signals, experimental
267 manipulations are critical to rigorously assess the mechanisms underlying their production. Schel et al.
268 (2013) exposed wild chimpanzees in the Budongo Forest, Uganda, to realistic moving snake models
269 and recorded their vocal behaviour.

270

271 In line with our framework, it is first critical to show that signalers exposed to model snakes signal
272 with a goal with a particular content (I). To infer the goal of the signaler, Schel et al. (2013)
273 investigated the cessation of alarm calling in chimpanzees. Theoretically, if the goal of alarm calling is
274 to warn others, signalers should persist until all potential receivers are safe. By implementing an
275 objective behavioural criterion of “safety” Schel et al. (2013) demonstrate that signal cessation was
276 not affected by the safety of the signaler, but instead when *receivers* were safe (see also Wich and de
277 Vries 2006). When alarm calling stopped, receivers were significantly more likely to be safe than
278 during the rest of the experimental trial.

279

280 Secondly, standardised criteria implemented in developmental child intentionality studies must be
281 applied to the signal to assess its voluntary nature and degree of recipient directedness. Schel et al.
282 (2013) showed that the production of certain types of alarm calls is influenced by the composition of
283 the social audience, as the arrival of friends but not non-friends in the area elicited an increase in the
284 production of these calls. Furthermore, analysis of audience checking behaviour, including gaze
285 alternation, suggested that signalers monitor and potentially take into account the current behaviour of
286 receivers when deciding to produce certain alarm calls. Hence chimpanzee alarm calls also appear
287 recipient directed.

288

289 The third and final criterion requires that receivers of the signal must regularly respond in a way that is
290 in line with the signaler's presumed intentions. However, such a demonstration does not require that
291 the receivers understand and represent the intentions of the signaler; and so does not imply any
292 attribution of a mental state to the signaler by the recipient. Currently the data available from the study
293 does not sufficiently satisfy this criterion, as Schel et al. (2013) did not directly explore the influence
294 of alarm calling on the receiver's behaviour. Nevertheless, certain observations do suggest that this
295 condition may also have been satisfied. When hearing conspecific alarm calls, receivers have been
296 observed to behave in a similar way as when they encounter predators naturally, including bipedal
297 scanning behaviour and tree climbing (Slocombe et al. unpublished data, Crockford et al. 2015, see
298 also Cheney and Seyfarth 1990). These behavioural observations suggest that the goal of the signaler,
299 in terms of warning group members of a threat, has potentially been met. However, more systematic
300 comparisons to baseline scanning behaviour indicating that the response was caused by the
301 communicated content are still required.

302

303 The above example of alarm calling in chimpanzees is not designed to demonstrate intentional
304 communication. Instead, it simply serves to illustrate that the proposed framework for assessing
305 intentional communication in animals is objective and realisable. Moreover, though there have been
306 previous valuable attempts to operationalise intentionality (Leavens et al. 2005, Liebal et al. 2006,
307 Vail et al. 2013, Hobaiter and Byrne 2014) these have been predominantly restricted to a single
308 modality (but see Hopkins et al. 2007), complicating multi-modal comparisons which are vital to
309 understanding intentional communication holistically. Our approach builds on existing work, but
310 crucially bridges the current gap that exists between modalities through being applicable to any
311 reliably and repeatedly observed communication signal.

312

313 III. CONCLUSION

- 314 1. The voluntary nature of human communication has long been considered a key, potentially
315 unique, feature of human cognition and language. In light of this, much comparative research
316 has attempted to unveil analogous or homologous forms of voluntary communication in
317 animals as a way to better understand what features are really unique to language and from this
318 how the language faculty may have evolved (Hauser et al. 2002, Fitch 2010). However,
319 advances in the field have been complicated by the scarcity of convincing evidence of
320 voluntary production of animal communication in the vocal domain (Wheeler & Fischer 2012,
321 Rendall and Owren 2013, though see Crockford et al. 2012). This gap in understanding has had
322 far reaching impacts regarding the predicted evolutionary route via which language may have
323 evolved, namely whether the origins of language were gestural or vocal.
- 324 2. We propose that the problem does not lie only in insufficient data. Additionally, it is bound up
325 with a preoccupation with questions about whether voluntary communicative acts in animals
326 are produced with the same sorts of cognitively complex intentions thought characteristic of
327 human communication – in particular, the intention to modify the mental states of receivers.
328 Although mental state attribution and its role in mediating signal production is an important
329 component of human intentional communication (Dennett 1983, Crockford et al. 2012), we
330 argue that focusing on this alone detracts from the equally informative examples of behaviour.
331 Moreover, the assumption that human communication must aim at changing mental states has
332 been challenged (Moore, 2015a).
- 333 3. How widely distributed first order intentionality is across the animal kingdom is a key question
334 that must be addressed if we are to i) understand the unique qualities of intentionality in
335 humans, ii) shed light on the modality and evolutionary route via which language evolved and
336 iii) understand more generally the adaptive benefit of intentional signalling in non-human
337 animals.

338 4. Critically, we provide the necessary framework to address first order intentionality, whether
339 analogous or homologous, across modalities and species giving rise to a unified and unbiased
340 understanding of the nature of intentional communication in animals.

341 **Acknowledgments**

342 This paper was seeded in a workshop “Deciphering the origins of intentional communication in
343 animals: an integrative approach” at University of Zurich. SWT, SEK, and IBG thank University of
344 Zurich’s Graduate Campus Grant for funding the workshop. We thank the anonymous reviewer for
345 constructive and helpful comments.

346

347

348

349 **IV. References**

350 Apperly, I.A., Riggs, K.J., Simpson, A., Samson, D. & Chiavarino, C. 2006. Is belief reasoning
351 automatic? *Psychological Science* 17: 841-844.

352 Bates, E., Benigni, L., Bretherton, I., Camaioni, L. & Volterra, V. 1979. The emergence of symbols:
353 Cognition and communication in infancy. New York: Academic Press.

354 Burkart, J. M., Roelli, C. & Richiger, R. 2015. When is behavior intentional? The case of proactive
355 prosociality. 6th EFP meeting, *Folia Primatologica*, 86, 253-254.

356 Byrne, R. 2016. *Evolving Insight*. Oxford University Press.

357 Call, J. & Tomasello, M. 2007. *The gestural communication of apes and monkeys*. Mahwah, New
358 York: Lawrence Erlbaum Associates.

359 Cartmill, E. A. & Byrne, R. W. 2007. Orangutans modify their gestural signaling according to their
360 audience's comprehension. *Current Biology* 17: 1345–1348.

361 Cheney, D.L., Seyfarth, R.M. 1990. *How monkeys see the world*. Chicago: University of Chicago
362 Press.

363 Corballis, M.C. 2002. *From hand to mouth: The origins of language*. Princeton University Press,
364 Princeton NJ.

365 Crockford, C., Wittig, R. M., Mundry, R. & Zuberbühler, K. 2012. Wild Chimpanzees Inform
366 Ignorant Group Members of Danger. *Current Biology* 22: 142–146.

367 Crockford, C., Wittig, R. M., & Zuberbühler, K. 2015. An intentional vocalization draws others'
368 attention: A playback experiment with wild chimpanzees. *Animal Cognition*, 18(3), 581-591.

369 Dennett, D.C. 1983. Intentional systems in cognitive ethology “The Panglossian paradigm” defended.
370 *Behavioral and Brain Sciences* 6: 343-390.

371 Dennett, D. C. 1988. Précis of *The Intentional Stance*. *Behavioral and Brain Sciences* 11: 495–546.

372 Fitch, W.T.F. 2010. *The Evolution of language*. Cambridge University Press, Cambridge UK.

373 Gaunet, F. & Massiou, F. 2014. Marked referential communicative behaviour, but no differentiation
374 of the “knowledge state” of humans in untrained pet dogs vs. 1-year-old infants. *Animal*
375 *Cognition* 17: 1137–1147.

376 Gómez, J. C. 1994. Mutual awareness in primate communication: a Gricean approach. In Parker,
377 Mitchell, & Boccia (eds.) *Self-Awareness in Animals and Humans*. Cambridge: CUP.

378 Grice, P. 1957. Meaning. *Philosophical Review* 64: 377-388.

379 Grice, P. 1982. Meaning Revisited. Pages 223–243 in N.V. Smith, ed. *Mutual Knowledge*. New York:
380 Academic Press.

381 Hauser, M. D., Chomsky, N. & Fitch, W.T.F. 2002. The Faculty of Language: What Is It, Who Has It,
382 and How Did It Evolve? *Science* 298: 1569–1579.

383 Hayes, C. 1951. *The Ape in Our House*. New York: Harper.

384 Heyes, C. & Dickinson, A. 1990. The intentionality of animal action. *Mind and Language* 5: 87-103

385 Hobaiter, C. & Byrne, R.W. 2014. The meanings of chimpanzee gestures. *Current Biology* 24, 1596-
386 1600.

387 Hopkins, W. D., Tagliatalata, J. P., & Leavens, D. A. 2007. Chimpanzees differentially produce novel
388 vocalizations to capture the attention of a human. *Animal Behaviour*, 73(2), 281–286.

- 389 Hopkins, W. D., Tagliabue, J. P., & Leavens, D. A. 2011. Do chimpanzees have voluntary control of
390 their facial expressions and vocalizations? In *Primate vocalizations and human language*
391 *Vocalisation, gestures, imitation and deixis in humans and non-humans* (pp. 71–88).
- 392 Hostetter, A. B., Russell, J. L., Freeman, H., & Hopkins, W. D. 2007. Now you see me, now you
393 don't: evidence that chimpanzees understand the role of the eyes in attention. *Animal Cognition*,
394 *48*(2), 87–96.
- 395 Hurford, J. R. 2007. *The origins of meaning: Language in the light of evolution*. Oxford University
396 Press, USA.
- 397 Jacob, P. 1997. *What Minds Can Do*. Cambridge: Cambridge University Press.
- 398 Jürgens, U. 1992. On the neurobiology of vocal communication. Pages 3-42 in Papousek H., Jürgens
399 U., Papousek, M., eds. *Nonverbal Vocal Communication*. Cambridge, UK: Cambridge University
400 Press.
- 401 Press.
- 402 Kenward, B., Folke, S., Holmberg, J., Johansson, A. & Gredebäck, G. 2009. Goal-directedness and
403 decision making in infants. *Developmental Psychology* *45*: 809-819.
- 404 Keysar B., Lin S. & Barr D.J. 2003. Limits on theory of mind use in adults. *Cognition* *89*: 25–41.
- 405 Leavens, D. A., Hopkins, W. D., & Thomas, R. K. 2004. Referential Communication by Chimpanzees
406 (Pan troglodytes). *Journal of Comparative Psychology* *118*: 48–57.
- 407 Leavens, D. A., Russell, J. L. & Hopkins, W. 2005. Intentionality as measured in the persistence and
408 elaboration of communication by chimpanzees (Pan troglodytes). *Child Development* *76*: 291–
409 306.
- 410 Liddle, B. & Nettle, D. 2006. Higher-order theory of mind and social competence in school-age
411 children. *Journal of Cultural and Evolutionary Psychology*, *4*(3-4), 231-244.
- 412 Liebal, K., Call, J., & Tomasello, M. 2004. Use of gesture sequences in chimpanzees. *American*
413 *Journal of Primatology*, *64*(4), 377–396.

414 Liebal K., Pika S. & Tomasello M. 2006. Gestural communication of orangutans (*Pongo pygmaeus*).
415 Gesture 6: 1-38.

416 Liebal, K., Waller, B. Burrows, A. & Slocombe, K. 2013. Primate communication: a multimodal
417 approach. Cambridge University Press.

418 Marler P.M, Dufty A, Pickert R. 1986. Vocal communication in the domestic chicken: II. Is a sender
419 sensitive to the presence and nature of a receiver? *Animal Behaviour* 34:194–198.

420 Mazzini, F., Townsend, S.W., Viranye, Z. & Range, F. 2013. Wolf howling is mediated by
421 relationship quality rather than underlying emotional stress. *Current Biology* 23, 1677–1680

422 McClung, J., Jentsch, I. & Reicher, S. 2013. Group Membership Affects Spontaneous Mental
423 Representation: Failure to Represent the Out-Group in a Joint Action Task. *PLoS ONE* 8: e79178

424 Millikan, R. 1984. Language, thought and other biological categories. Cambridge (Mass), MIT Press.

425 Moore, R. 2014. Ontogenetic constraints on Paul Grice's theory of communication. In Danielle
426 Matthews (ed.) *Pragmatic Development in First Language Acquisition*. Amsterdam: John
427 Benjamins. pp. 87-104.

428 Moore, R. 2015a. A common intentional framework for ape and human communication. *Current*
429 *Anthropology*, 56(1), 71-72.

430 Moore, R. 2015b. Meaning and ostension in great ape gestural communication. *Animal Cognition*.

431 Notman, H., & Rendall, D. 2005. Contextual variation in chimpanzee pant hoots and its implications
432 for referential communication. *Animal Behaviour*, 70(1), 177-190.

433 Pika, S. & Liebal, K. 2012. (Eds.), *Developments in Primate Gesture Research*. Amsterdam: John
434 Benjamins Publishing Company.

435 Povinelli, D., Theall, L., Reaux, J., Dunphy-Lelii, S. 2003. Chimpanzees spontaneously alter the
436 location of their gestures to match the attentional orientation of others. *Animal Behaviour*, 65, 1–9

437 Rendall, D. & Owren, M.J. 2013. Communication without meaning or information: abandoning
438 language-based and informational constructs in animal communication theory. Pages 151-188 *in*

439 U.E. Stegmann, ed. *Animal communication theory: Information and influence*. Cambridge
440 University Press, Cambridge UK.

441 Rendall, D., Cheney, D. L. & Seyfarth, R. M. 2000. Proximate factors mediating “contact” calls in
442 adult female baboons (*Papio cynocephalus ursinus*) and their infants. *Journal of Comparative*
443 *Psychology* 114: 36–46. doi:10.1037//0735-7036.114.1.36

444 Ristau, C. 1991. Aspects of the cognitive ethology of an injury-feigning bird, the piping plover
445 in *Cognitive Ethology: The Minds of Other Animals*. ed. C. Ristau, Lawrence Erlbaum Associates,
446 Hillsdale.

447 Russell, J. L., Braccini, S., Buehler, N., Kachin, M. J., Schapiro, S. J., & Hopkins, W. D. 2005.
448 Chimpanzee (*Pan troglodytes*) intentional communication is not contingent upon food. *Animal*
449 *Cognition*, 8(4), 263–272.

450 Savalli, C., Ades, C. & Gaunet, F. 2014. Are dogs able to communicate with their owners about a
451 desirable food in a referential and intentional way? *Plos ONE* 9: e111387.

452 Schel, A.M., Townsend, S.W., Machanda, Z., Zuberbühler, K. & Slocombe, K.E. 2013. Chimpanzee
453 alarm call production meets key criteria for intentionality. *PLoS ONE* 8: e76674.

454 Scott-Phillips, T.C. 2015a. Nonhuman primate communication, pragmatics, and the origins of
455 language. *Current Anthropology* 56: 56-80.

456 Scott-Phillips, T. C. 2015b. Meaning in animal and human communication. *Animal Cognition*, 18(3),
457 801-805.

458 Seyfarth, R. M., Cheney, D. L. & Marler, P. 1980. Monkey responses to three different alarm calls:
459 evidence of predator classification and semantic communication. *Science* 210: 801–803.

460 Slocombe, K. E., Kaller, T., Turman, L., Townsend, S.W., Papworth, S & Zuberbühler, K. 2010.
461 Production of food-associated calls in wild chimpanzees is dependent on the composition of the
462 audience. *Behavioural Ecology and Sociobiology* 64: 1959-1966.

463 Slocombe, K. E., Waller, B. M. & Liebal, K. 2011. The language void: the need for multimodality in
464 primate communication research. *Animal Behaviour* 5: 919-924.

465 Sperber, D. & Wilson, D. 1995. *Relevance: Communication and Cognition*, Second Edition,
466 Oxford/Cambridge: Blackwell Publishers.

467 Sperber, D. 2000. Meta-representations in an evolutionary perspective. In Sperber (ed.) *Meta-*
468 *representations: A Multidisciplinary Perspective*. Oxford: OUP.

469 Strawson, P.F. 1964. Intention and convention in speech acts. *Philosophical Review* 73: 439-460.

470 Tomasello, M. 2008. *Origins of Human Communication*. MIT Press.

471 Vail, A.L., Manica, A. & Bshary, R. 2013. Referential gestures in fish collaborative hunting. *Nature*
472 *Communications* 4: 1765 (1–7).

473 Wheeler, B. C. & Fischer, J. 2012. Functionally referential signals: A promising paradigm whose time
474 has passed. *Evolutionary Anthropology* 21: 195–205.

475 Wich S.A. & de Vries H. 2006. Male monkeys remember which group members have given alarm
476 calls. *Proceedings of the Royal Society Series B* 273: 735–740.

477 Wimmer, H & Perner, J. 1983. Beliefs about beliefs: representation and constraining function of
478 wrong beliefs in young children’s understanding of deception. *Cognition*, 13, 103-128.

479 Wit, S. & Dickinson, A. 2009. Associative theories of goal-directed behaviour: a case for animal–
480 human translational models. *Psychological Research* 73: 463–476.

481 Yerkes, R. M. & Yerkes, A. W. 1929. *The great apes: a study of anthropoid life*. New Haven: Yale
482 University Press.

483 Zanjonc, R.B. 1965. Social facilitation. *Science*, 149, 269-274.

484 Zuberbühler, K. 2005. The phylogenetic roots of language: evidence from primate communication and
485 cognition. *Current Directions in Psychological Science* 14: 126–130

486 Zuberbühler, K. 2008. Audience effects. *Current Biology*, 18, R190.
487
488

490 Table 1: The criteria for intentional communication in animals pertinent to step 2 in the new
 491 framework. Amended from Schel et al. (2013).
 492

Criterion	Explanation
Social use	The signal is directed at a recipient. This can be assessed at various levels: <ol style="list-style-type: none"> 1. Presence/absence audience effect: the signal is only produced in the presence of a recipient. 2. Composition of audience: the signal is only produced in the presence of certain recipients (e.g., kin, dominants, friends) 3. Behaviour of audience: signal production is contingent on the behaviour of the recipient
Sensitivity to attentional state of recipient	Visual signals are only produced in the field of view of recipients. If signaler does not have a recipient's visual attention, tactile or auditory signals should be produced. This can also be considered a level (3) of audience effect.
Manipulation of attentional state of recipient	Before a visual signal is produced, attention-getting behaviours are directed towards a recipient who is not visually attending to the signaler or the signaler moves itself into the line of view of a recipient (Liebal et al. 2004).
Audience checking and gaze alternation	Signaler monitors the audience and visually orients towards the recipient before producing a signal. If a third entity is involved, gaze alternation may occur between recipients and this entity.