

1 **ROUGH-AND-TUMBLE PLAY AS A WINDOW ON ANIMAL COMMUNICATION**

2

3 **Elisabetta Palagi^{1,2,3}, Gordon M. Burghardt^{1,4}, Barbara Smuts^{1,5}, Giada Cordini^{1,2}, Stefania**
4 **Dall'Olio², Hillary N. Fouts^{1,6}, Milada Řeháková-Petrů^{1,7}, Steve Siviy^{1,8}, and Sergio Pellis^{1,9}**

5

6 ¹ NIMBioS - National Institute for Mathematical and Biological Synthesis - University of Tennessee -
7 Knoxville (Tennessee, USA)

8 ² Centro Ateneo Museo di Storia Naturale - Università di Pisa - Pisa (Italy)

9 ³ CNR, Istituto di Scienze e Tecnologie della Cognizione - Roma (Italy)

10 ⁴ Departments of Psychology and Ecology & Evolutionary Biology – University of Tennessee,
11 Knoxville (Tennessee, USA).

12 ⁵ Department of Psychology, University of Michigan (USA)

13 ⁶ Department of Child and Family Studies – University of Tennessee, Knoxville (Tennessee, USA)

14 ⁷ Tarsius, o.s., Decin Zoo, Czech Republic.

15 ⁸ Faculty of Psychology - College of Gettysburg (Pennsylvania, USA)

16 ⁹ Department of Neuroscience, University of Lethbridge, Alberta, Canada

17

18

19 **ABSTRACT**

20 Rough-and-tumble play (RT) is a widespread phenomenon in mammals. Given that it involves
21 competition, whereby one animal attempts to gain some advantage over another, RT runs the risk of
22 escalation to serious fighting. Even though the competition is typically curtailed by some degree of
23 cooperation, a variety of signals help to negotiate potential mishaps during RT. This review provides a
24 framework for such signals, showing that they range along two dimensions: one from signals borrowed
25 from other functional contexts to ones that are unique to play, and the other from purely emotional
26 expressions to highly cognitive constructions. Some lineages of animals have exaggerated the inter-play
27 between the emotional and cognitive aspects of play signals, yielding admixtures of communication that
28 have led to very complex forms of RT. This complexity has been further exaggerated in some lineages
29 by the development of play specific novel gestures that can be used not only to negotiate playful mood
30 but also to entice reluctant partners. These play-derived gestures may provide new mechanisms by
31 which more sophisticated forms of communication can evolve. An example in our own lineage may be
32 the transition from manual gesturing to verbal speech. Therefore, the sophisticated versions of RT and
33 playful communication provide a window into the study of social cognition, emotional regulation and
34 the evolution of communicative systems.

35

36

37 **INTRODUCTION**

38 Defining play is a difficult matter. Compared to so-called “serious” behavior patterns, whose
39 modalities and functions are more easily detected, play remains an intriguing challenge. Burghardt
40 (2005, 2011) developed five criteria to identify play. Play is behavior that is not completely functional in
41 the form or context in which it is performed because it does not seem to contribute to current survival
42 (first criterion). Play is spontaneous, voluntary, intentional, pleasurable, rewarding, reinforcing, or
43 autotelic (“done for its own sake”) (second criterion). Compared to other ethotypic behaviors, play is
44 incomplete, exaggerated, awkward, or precocious and it generally involves patterns modified in their
45 form, sequencing, or targeting (third criterion). During a play session, the behavioral pattern is
46 performed repeatedly but not in a manner that is rigidly stereotyped (fourth criterion). Play is initiated
47 when animals are relatively free from environmental and social stressors (fifth criterion).

48 Beyond its definition, among all social activities, social play stands out for its versatility,
49 plasticity, and unpredictability (Fagen 1993; Burghardt 2005, 2012; Špinka et al., 2001; Palagi et al.,
50 2007). Nonetheless, social play does follow rules that, if violated, can lead to serious aggression (Pellis
51 & Pellis 1998a; Pellis et al., 2010). While rules are followed in both free play (e.g., play fighting) and
52 structured games (e.g., rugby matches), the nature of the rules differs (Power 2000, Burghardt 2005).
53 Structured games, unlike free play, are built on *a priori* and written rules and the participants have to
54 follow such pre-set rules to avoid being penalized in some form. In animal and child “free play” rules
55 exist and are often based on instinctive and neural mechanisms, but they are not formalized and fixed
56 (Pellegrini 2009). Each new play session is a new item on the agenda during which the ‘rules’ are
57 continually being redefined. Partners, age, context, physical and emotional states, etc. are continuously
58 shifting. Thus, the formulation and application of such *hic et nunc* codes depend on vast arrays of
59 variables that can change continuously. Indeed, the rules are rearranged and re-negotiated as a function

60 of the players involved (gender, rank, age, size, kin) and the kind of play performed (tickling,
61 locomotor-rotational activities, fighting). Finally, unlike structured games where the rules may be
62 enforced by a third party (e.g., umpire), during free play, not only are the rules negotiated by the
63 participants, but so is the enforcement of the agreed upon rules. Therefore, managing new playful
64 interactions requires sophisticated and complex communicative skills - skills which themselves may
65 need to change as a play bout unfolds. Thus, social play involves considerable communicative effort,
66 improvisation, strategic timing, and creativity. For these reasons, play may be more mentally demanding
67 than engaging in many other non-aggressive behavioral contexts. Indeed, comparative studies of
68 primates have shown that those species that engage in more social play also have an enlargement of
69 several of the brain areas involved in regulating play. No such species differences in brain size exist
70 among species that differ in the amount of non-social (solitary) play (Graham and Burghardt 2010).
71 Because of these demands on flexibility and improvisation during social play, this behavior has been
72 hypothesized to be the engine of much behavioral innovation (Fagen 1993). For the present purpose, we
73 suggest that it is also the reason why social play is an ideal context to study communication and
74 cognition.

75
76

77 **1. Why communication is fundamental for rough-and-tumble (RT) play**

78 Social play, especially in its complex forms focused on here, is intimately associated with
79 communication. Indeed, play communication, we argue, may be among the most complex
80 communication system seen in nonhuman and human animals. In its most elemental form,
81 communication can be characterized as a behavior in which it is to the real or perceived advantage of the
82 signaler (or the signaler's group) for it to get its message across to another organism (Burghardt, 1970).
83 The prolonged reciprocal interactions that occur during play involve a situation in which the players are,

84 often simultaneously, both signalers and receivers. Often dyadic in nature, play that involves teams (as
85 in the aforementioned rugby match) incorporates the broader aspect of the definition of communication
86 given above.

87 Rough-and-tumble (RT) is, arguably, the most complex form of social play in animals, including
88 children, because it involves physical contact between partners and may include patterns typical of real
89 fighting. Although there are rules of interaction that differ between RT and its serious counterparts
90 (Pellis et al. 2010), many ambiguous situations arise, such as when a playful attack occurs unexpectedly.
91 In such cases, additional information, such as that provided by particular signals, are important (Aldis
92 1975). Although not invariably unambiguous themselves (Pellis and Pellis 1996, 1997), in many
93 circumstances such signals can reduce the uncertainty arising from contact during play (Palagi 2008,
94 2009). Specific actions, gestures, gaits, vocalizations, facial expressions, and even odors may
95 communicate the playfulness of a potentially dangerous act (Fagen 1981, Bekoff 2001a, Palagi 2006).
96 Signals can help to avoid escalation to real aggression and may prolong play (Burghardt 2005, Waller
97 and Dunbar 2005, Mancini et al. 2013a). Bekoff (1995) stressed the importance of play signals as
98 "punctuation" during playful interactions, especially when play includes elements of hostility. Moreover,
99 communicative signals can also have a major role in expressing positive emotions, which can make the
100 session pleasurable and rewarding for the players (Kuczaj and Horback, 2013). In this view, managing a
101 playful interaction successfully can favor the development of cooperation beyond the play session itself
102 (Palagi and Cordoni 2012).

103 RT uses both movements and signals recruited from other functional behaviors (e.g., predatory,
104 antipredatory, mating, intra-species agonism) (Bekoff and Byers 1981; Fagen 1981, 1993; Pellis 1988)
105 and others exclusive to play (Petrů et al. 2009). Examples of the former are chasing, pouncing (derived
106 from fighting) and lip-smacking (derived from grooming). Examples of the latter are canine play bows

107 (Bekoff 1995), head rotation (Petrů et al. 2009), tickling (van Lawick-Goodall 1968), vocalizations
108 (Rasa 1984) and play faces (Pellis and Pellis 1997, Palagi 2008) (Figure 1).

109 Communication during RT can also vary along another dimension. At one extreme are behaviors
110 such as facial expressions that occur independently of the actions of the partner, and so appear to be
111 primarily determined by the emotional state of the performer (Cordoni and Palagi 2011; Pellis et al.,
112 2011). At the other extreme are movements, such as hand gestures in great apes, which the animals use
113 in contexts where they appear to be soliciting the attention of a potential play partner, and so are closely
114 linked to the behavior of the partner (Horowitz, 2009). Other signals fall in-between these extremes
115 (Figure 1). In practice, many play behaviors may fall closer to the middle of one or the other of these
116 dimensions. This framework is useful because it includes many different aspects of play communication,
117 some of which have ancient evolutionarily roots and are, therefore, shared among many species
118 (plesiomorphic), as well as others that take highly variable forms across different species (apomorphic).
119 This inclusive approach facilitates cross-species comparisons and identification of homologous and
120 derived/convergent processes in the evolution of play. Although RT, play fighting, and tussle play have
121 been described in many eutherian and marsupial mammals as well as in other vertebrates, including
122 birds and frogs (Burghardt, 2005), here we focus on the extensive research available on the most
123 commonly studied mammalian taxa: rodents, carnivores, non-human primates, and humans.

124

125 **2. RT communication patterns recruited from other functional behaviors**

126 The incorporation and elaboration of communication signals across functional behavior systems is
127 well known in the contexts of feeding, courtship, agonistic attack/defense, and parent-offspring
128 interactions, and was termed ritualization by the early ethologists (Cullen 1966, Thorpe 1966,
129 Burghardt, 1973). That play behavior may both recruit the use of ritualized behavioral elements and also

130 provide the source for other ritualized behavior has not been sufficiently recognized (Burghardt, 2012)
131 and thus merits increased research attention.

132 During serious fighting animals use tactics of attack to deliver blows or bites and use tactics of
133 defense so as to block those strikes. Moreover, attacking animals face the threat of retaliation, as a
134 successful parry can be followed by a counterattack by the original defender (Geist 1978). To effectively
135 attack while minimizing the likelihood of retaliation, offensive maneuvers frequently incorporate a
136 defensive component (Pellis 1997). The situation is different in RT: for RT to remain playful it has to
137 sometimes be reciprocal, so the animals' maneuvers often work to facilitate role reversals (i.e.,
138 successful counterattacks) (Pellis et al. 2010). To do this, rats, monkeys and other species will playfully
139 attack, but do so without an associated defensive component, and this leads to an increase in the
140 probability of a successful counterattack by the recipient of the attack, and so a role reversal (Pellis and
141 Pellis 1998a).

142 *Rodents.* During RT, rats attack and defend the nape of the neck, which if contacted is nuzzled
143 with the snout (Pellis and Pellis 1987, Siviy and Panksepp 1987). As juveniles, the most common tactic
144 to block the attack to the nape is to roll over to supine, pressing the nape against the ground and using
145 the forepaws to fend off further attacks. The attacking rat, in turn, stands over the supine partner, using
146 its forepaws to restrain the partner while maneuvering to gain access to the nape (Pellis and Pellis 1987).
147 Leverage to control the supine partner is provided by keeping the hind legs firmly planted on the ground,
148 yet juveniles will frequently interject a self-defeating movement when in this on-top position. They will
149 stand on the squirming supine partner with all four feet, compromising their postural stability (Foroud
150 and Pellis 2002, 2003). Indeed, when the supine partner lunges up at the other's nape, the probability of
151 a successful role reversal (so that the animal standing on top ends up on its back) is about 30% when the

152 partner's hind feet are anchored on the ground, but jumps to over 70% when standing with all four feet
153 on the supine rat (Pellis et al. 2005).

154 But not all species appear to be so restrained in the use of offensive tactics during RT (Thompson
155 1998). Some species, such as the South American rodent, the degu (*Octodon degu*) combine defense
156 with attack in play as well as in serious fighting, yet play fights do not proceed to all out fighting. This
157 species appears to use a different strategy to ensure playful reciprocity – once an attack tactic is
158 successfully delivered, the performer does not follow this up with further attack, but rather stops, and
159 allows the recipient to recuperate and counterattack (Pellis et al. 2010). In serious fighting a successfully
160 delivered attack is followed by further attack. There are, then, a variety of ways in which species have
161 evolved strategies for ensuring reciprocity (Pellis et al. 2010). In rodents, with a paucity of play signals
162 (see below), the role of postural and movement-related facilitators of play is probably greater than in
163 lineages with a richer repertoire of play signals. Thus, in rats, the fighting movements performed during
164 play incorporate self-handicapping postures, and in species like the degu, play facilitating postures can
165 be performed after a successful attack (Figure 1).

166 *Carnivores.* Domestic dog RT involves several different types of movements (Bauer and Smuts
167 2007, Handelman 2008), which are not strict categories, since elements from any one type may be
168 included in or interspersed with other types. RT among adult wolves has not been systematically
169 described, but it appears to involve all of the play behaviors shown by dogs and, probably, a few others
170 unique to wolves (Cordoni 2009). In two five-week old wolf cubs, contact games are mainly
171 characterized by softly biting the partner's ears, cheeks, limbs, and tails; after the second month of age,
172 the bites are primarily directed towards the throat and shoulders combined with shake movements,
173 embracement, and pouncing (Feddersen-Petersen 1991). A similar ontogenetic shift in play biting
174 performance can be observed also in polecats (*Mustela putorius*) (Poole 1978). For wolves, the first

175 four-six weeks of life are also characterized by high frequencies of games involving mimicking, during
176 which the two cubs imitate each other's facial expressions (muzzle-wrinkling, lip-retraction) without
177 being in physical contact (Feddersen-Petersen 1991). In contrast to wolves, for poodles, games in which
178 they mimic one another mainly involve playful communication in the acoustic modality (e.g. bark
179 games). This form of acoustic play reaches its peak during the fourth month of life (Feddersen-Petersen
180 1991).

181 Drea et al. (1996) found that in spotted hyenas (*Crocuta crocuta*) playful bites lasted longer
182 compared to ones performed during aggression and were never associated with rapid side-to-side head
183 shaking. Coyotes (*Canis latrans*) punctuated their vigorous play sessions with patterns recruited from
184 the affiliative behavioral repertoire (e.g., tail wagging) (Way 2007). All these findings clearly show that
185 the plasticity (e. g., modality, intensity, body targets, duration, and timing) characterizing the
186 performance of patterns recruited from other functional contexts may in itself represent a playful signal.
187 Such plasticity appears to be lacking in the play of golden jackals (*Canis aureus*), which is highly
188 stereotyped and has a paucity of communicative elements; in fact, during the first four-six weeks of life,
189 play fighting in cubs frequently escalates into serious fighting (Feddersen-Petersen 1991).

190 Henry and Herrero (1974) described RT in young wild black bears from the ages of four months to
191 four years. In low intensity RT, bites were quickly released or performed without contact. Moreover,
192 these authors pointed out that social play in young bears includes many motor patterns also
193 characteristic of canid play, including the play face, face-pawing, neck-biting in an attempt to push the
194 partner over, placing the front paws on the partner's back or shoulders, and rearing up on the hind legs
195 facing the partner accompanied by paw-sparring.

196 *Nonhuman primates.* Most of the research on RT and playful communication on primates has been
197 conducted on monkeys and apes (haplorrhines). However, data from a wider array of primate taxa are

198 needed for a more comprehensive understanding of the possible roles of play communication and the
199 cognitive skills required supporting such communication (Armstrong 1985). Lemurs, which are
200 relatively small brained, form an independent primate radiation and represent the most ancestral group-
201 living primates (Tattersall 1982). Comparing lemurs to the haplorrhines is especially useful because
202 these two distantly related primate groups share basic features of natural history. The ringtail lemur
203 (*Lemur catta*) is a diurnal and highly terrestrial species, which forms multimale/multifemale social
204 groups characterized by strong female dominance and male dispersal (Jolly 1966). The tail of this
205 species, with its white and black rings, is used to communicate and regulate many aspects of social life.
206 The "stink fights" engaged in by males during their agonistic interactions are the most striking example
207 (Jolly 1966). Males place their tails between the legs and upward in front of the torso and anoint them
208 with the secretion produced by specialized antebrachial glands on wrist and forearm (*anoint-tail*). Then,
209 the animal may repeatedly flick the tail downward over the top of its head to spread the odor secretion
210 (*wave-tail*). During the agonistic wave-tail pattern, with his ears flattened against the top of his head, the
211 male faces and gazes at the opponent. Mature males also anoint and wave their tails toward females as
212 signals of appeasement or even submission during courtship (solicitation of copulation; Jolly 1966).
213 There is also a playful version of the communication pattern involving tail use (Jolly 1966): a good
214 example of a pattern recruited from other functional contexts to communicate during play.

215 During RT, ringtailed lemurs anoint their tails neither facing the playmate nor even gazing at the
216 playmate (tail-play). Infants begin to perform tail-play during the weaning period (about 6 months;
217 Palagi et al. 2002). Analysis of the dynamics of RT in juvenile ringtail lemurs indicates that such play
218 strongly resembles real aggression (Pellis and Pellis 1997). In a number of species, adult RT has been
219 reported to be rougher, having a greater likelihood of escalation into serious fighting (Fagen 1981, Pellis
220 2002, Palagi and Cordoni 2012). However, the low levels of escalation found in lemurs (Palagi 2009)

221 suggest that ringtailed lemurs are able to cope with possible ambiguous situations, with tail-play
222 probably having a role. During play, males generally direct tail-play mostly toward females, which can
223 be very aggressive towards them (Jolly 1966). Hence, playing with females may be particularly risky for
224 males, who need to clearly signal their own “playful intentions” to avoid misinterpretation. Ringtailed
225 lemurs also frequently use tail-play when playing with less-familiar group members (as determined by
226 low grooming rates). When play occurs between potentially dangerous partners, RT is often
227 characterized by a redundancy of signals (Bekoff 1974, Henry and Herrero 1974, Power 2000). In fact,
228 RT between two individuals, which socially interact at a very low frequency, may be particularly unsafe
229 due to the limited information (physical strength, self-handicapping skill, and movement rapidity) they
230 have about each other. Social play is often contagious, and so can attract additional partners leading to
231 multi-animal bouts of play (Hayaki 1985; Miklósi 1999). Managing polyadic sessions may be
232 considered as especially challenging, making the appropriate use of communication particularly
233 important. The hypothesis seems to be supported by the prominent use of tail-play during polyadic
234 sessions among adult ringtail lemurs. In conclusion, tail-play may represent a useful tool for
235 communicating the motivation to play in this species (Figure 1).

236 *Humans.* In humans, structural descriptions of play have focused on three main characteristics:
237 exaggeration, sequence variability and incompleteness (Pellegrini 2009). Specific body movements
238 alone, like running and jumping, are not necessarily indicative of play. Instead play movements are
239 recognized when associated with a constellation of features, for example exhibiting a play face while
240 jumping, running in an exaggerated manner (e.g., leaping strides), or running with a variable sequence
241 (e.g., zig-zagging). Incomplete body movements, like punching near a play partner’s arm but not
242 actually making contact, are also used to communicate during play. Blurton Jones (1972), in an
243 observational study of 2- and 4-year-olds, found in a factor analysis that the RT play factor had high

244 loadings for laughing-play face, run, jump, hit at, and wrestle. RT play was not associated with
245 aggression, and the aggression factor had high loadings for different body movements including hit,
246 push, and take-tug-grab. Unfortunately, body movements involved in play have not been a major focus
247 of research among humans. While human ethologists (see Blurton Jones 1972) initially focused on the
248 movements performed by children when playing, most contemporary research on the play of children
249 has focused less on the structural components of play and more on its social aspects.

250

251 **3. RT communication patterns exclusive to play**

252 RT varies in complexity across species (Pellis and Pellis 1998b). More complex RT seems related
253 to more complexity in the specific play signals used to manage play sessions in some lineages, such as
254 in Primates and Carnivores (see below).

255 *Rodents.* In rodents, irrespective of the complexity of play, there is little evidence for the existence
256 of specific play signals. There has been the suggestion of a play specific odor in one species of vole
257 (*Micotus agrestis*) (Wilson 1973) and during RT rats emit 50 kHz vocalizations (Knutson et al. 1998).
258 However, play-specific odors have not been confirmed in other species, and the use of 50 kHz
259 vocalizations is not restricted to play, but rather these calls are emitted in a variety of positively affective
260 situations (Burgdorf et al. 2008). It has yet to be determined whether these calls are performed
261 specifically to solicit play or are simply a reflection of positive mood. More typically associated with
262 play in rodents is the presence of locomotor-rotational movements (van Oortmersen 1971, Pellis and
263 Pellis 1983), which, like the case for bonobos (see above), appear to stimulate playful activity in the
264 observer. Indeed, playfulness in one rat is contagious, making other animals engage in more play even if
265 they have ceased playing due to fatigue or satiation (Pellis and McKenna 1995; Reinhart et al. 2006).

266 *Carnivores.* The play bow is the most familiar carnivore specific play signal. The performer bows
267 in front of the playmate while wagging its tail and play panting (breathy exhalation) (Bekoff 1995). Play

268 bow is shown by most canids as well as by lions (Schaller 1972) and, surprisingly, by Arabian babblers
269 (*Turdoides squamiceps*) (Pozis-Francois et al. 2004). An anecdotal report on wolves illustrates the
270 importance of the play bow as a signal to promote friendly contact (Stahler et al. 2002). A 2.5 year old
271 male (#21), from a neighboring pack, attempted to join the all-female Druid pack. Male #21 followed
272 the Druid females and firstly interacted with a nearly full-grown pup by wagging its tail and eliciting
273 several play bows in response. Next the alpha female approached #21 and she play bowed three times.
274 About one hour later the beta female approached #21 for the first time by sniffing his neck and play
275 bowing several times. Then the alpha female started jumping around #21 by giving a series of play bows
276 too. Wolf #21 remained with the Druids as their alpha male for the rest of his life. Thus, the Druid
277 females used play signals both during their initial interactions with the unfamiliar male and also,
278 apparently, as "acceptance" signals as their interactions became more intimate.

279 Many carnivores also display facial signals during play. Young black bears (*Ursus americanus*)
280 exhibit a puckered-lip facial expression and a distinctive ear posture ('crescent ears,' in which the pinnae
281 face to the side and stand out perpendicularly from the side of the head). Head butting, play nipping and
282 a relaxed, open mouth also seem to function as play signals. Five different ear postures were shown
283 during RT in black bears, including flattening of the ears, which occurred when RT became more
284 intense; this signal usually terminated play (Henry and Herrero, 1974).

285 Fox (1970) described the early development of play faces in grey (*Urocyon cinereoargenteus*), red
286 (*Vulpes vulpes*) and arctic (*Alopex lagopus*) foxes as well as in coyotes (*Canis latrans*) and wolves
287 (*Canis lupus*). He emphasized "...that the facial expressions of the wolf and coyote are much more
288 variable and show greater degrees of graduation...in contrast to the more stereotyped and less variable
289 expressions of the foxes" (p. 59). Domestic dogs clearly illustrate this graduation in intensity of the
290 canine play face. At low intensity, the mouth is relaxed, so that only the upper parts of the frontal lower

291 teeth are visible. At a slightly higher intensity, the mouth is opened wider so that most or all of the
292 bottom teeth can be seen. At highest intensity, the mouth is wide open so that both top and bottom teeth
293 are visible (Handelman 2008). The first two faces may be analogous to the primate play face and the
294 third to the full play face of primates (see below). The degree of mouth opening has not been studied as
295 a function of the context or accompanying behaviors. Informal observations suggest that the play face is
296 common during play invitations, running and chasing and sometimes during brief pauses in play,
297 whereas the full play face tends to appear in conjunction with bite intentions or bite attempts and
298 attempts to parry bites (Smuts, personal observation). During jaw sparring, dogs fence with wide-open
299 mouths (Handelman, 2008) and an audible 'clicking' occurs when teeth clash. However, in contrast to a
300 real bite attempt where the head would be thrust forward toward the other dog, in jaw sparring the heads
301 tend to tip back and forth sideways, so that teeth do not approach the other dog's skin (Smuts, personal
302 observation).

303 *Non-human primates.* In some species of cercopithecines, head and torso rotations are body
304 movements peculiar to play (Bekoff 1974, Wilson and Kleiman 1974, Byers 1984, Donaldson et al.
305 2002, Petrù et al. 2008). As some of them may serve as play signals, they are sometimes labeled "play
306 markers". In Hanuman langurs, a third of the play repertoire consists of patterns that are unique to play
307 (Petrù et al. 2009). Since they have no counterpart in other types of behavior, either in adulthood or
308 other stage of ontogeny, they cannot serve to train specific skills needed in "serious" behavior. Some of
309 these play-specific patterns may have a signaling function, as is probably the case of play face, eyes
310 closing, or play gallop. Thus, they do not have a function beyond the boundary of play, but rather serve
311 to keep the play going and thus allow other play elements to be performed and fulfill their function.
312 Some other patterns (play tumble, head rotation, somersaults, flips, leaps) are also unique to play and
313 may, therefore, serve as play signals. However, specialized signals are usually encoded in rather

314 stereotypic movements to transmit information reliably (Morris 1966, Zahavi 1979, Hinde 1982,
315 McFarland 1987) but Petrů et al. (2009) found these patterns very variable. Moreover, they were present
316 in solitary play as well, so how these actions function as possible play facilitating signals remains to be
317 resolved.

318 The typical expression of social play is the relaxed, open-mouth display (or play face, PF), which
319 can be performed in two different configurations (van Hooff and Preuschoft 2003). In some species,
320 such as in bonobos and chimpanzees (*Pan spp.*), geladas (*Theropithecus gelada*) and Tonkean macaques
321 (*Macaca tonkeana*), play face (PF) and full play face (FPF) represent two different degrees of the same
322 playful expression. In the PF, the mouth is opened with only the lower teeth exposed, whereas in the
323 FPF the mouth is opened in a relaxed mood with both upper and lower teeth exposed (Palagi 2008,
324 Palagi and Mancini 2011). It has been hypothesized that these playful expressions are ritualized versions
325 of the biting movement that precedes the play bite, a very common behavior in RT (van Hooff and
326 Preuschoft 2003, Palagi 2006). The PF is widespread in almost all primate species, and for this reason it
327 is considered to be the most ancestral configuration of the playful facial displays in this *taxon*. On the
328 other hand, the presence of FPF seems to follow a patchy distribution, apparently random with respect to
329 phylogeny (Preuschoft and van Hooff, 1997). Humans (*Homo sapiens*), bonobos (*Pan paniscus*) and
330 gorillas (*Gorilla gorilla*) habitually use FPF, whereas chimpanzees (*Pan troglodytes*) use the classical
331 PF (Palagi 2006, Palagi et al. 2007, Cordoni and Palagi 2011, Palagi and Cordoni 2012).

332 In some cercopithecine species, the use and structure of particular facial expressions can converge
333 as a function of their species-typical baseline levels of tolerance and affiliation (Thierry et al. 1989, Petit
334 et al. 2008). For example, in Sulawesi macaques (*Macaca nigra*), mandrills (*Mandrillus sphinx*), and
335 geladas (*Theropithecus gelada*), all well-known as the most tolerant cercopithecine species, the FPF is
336 not a more intense version of PF but derives from the convergence between PF and the silent-bared teeth

337 display, a facial expression used for affiliative purposes (van Hooff and Preuschoft 2003, Bout and
338 Thierry 2005).

339 The 20 species of macaques are all organized in multi-male, multi-female groups but they vary on
340 a gradient ranging from more intolerant (despotic) to more tolerant (egalitarian) social systems (Thierry
341 2000). These different social styles influence a wide range of behaviors including aggression and
342 affiliation patterns, dominance relationships, and play (Thierry 2000, Reinhart et al. 2010, Ciani et al.
343 2012). In a comparative study on the genus *Macaca* the use of playful signals has been investigated
344 according to the different levels of tolerance characterizing two species placed at opposite ends of the
345 gradient: *Macaca fuscata* and *Macaca tonkeana*. This study, for the first time, demonstrates the presence
346 of FPF in Japanese macaque, a highly despotic species, thus suggesting that making a clear-cut
347 distinction between species that perform this signal and species that do not is not appropriate. Even
348 though FPF has been observed in Japanese macaques there is a striking difference in the frequency with
349 which this playful signal is used between *M. fuscata* and *M. tonkeana*. In the more tolerant Tonkean
350 macaque about 90% of all open mouths are of the FPF version (Pellis et al. 2011), which is substantially
351 higher than in the more despotic Japanese macaque (Palagi, unpublished data).

352 Whatever the origins and distribution of playful facial expressions may be, they have a pivotal role
353 in managing playful interactions. The use of playful facial expressions is important to avoid any
354 misunderstanding, cope with a playful interaction successfully, promote social affiliation, and favor
355 cooperation (Pellis and Pellis 2009). Adult geladas make an intense use of FPF that, from a perceptive
356 point of view, is a more effective and less ambiguous because it can be visually perceived at longer
357 distances compared to PF (Palagi 2008, Palagi and Mancini 2011). FPF may also have an important role
358 especially when play occurs in a social situation that is highly tense, such as that following intra-group
359 aggression. Similarly, in humans an increase in distress may be prevented by smiling appropriately (as a

360 corrective response), thus maintaining a cooperative mood during play (van Hooff 1989). In this view,
361 human laughter and FPF in geladas (and other primate species) may be used as a cognitively demanding
362 mechanism to offset the chance of aggression (Figure 1). Play signals are not only the expression of an
363 internal emotional state, but also, as has been shown in humans, they can have a manipulative function
364 (Gervais and Wilson 2005). There is evidence, for example, that great apes can use play signals in a
365 strategic manner during play (Figure 1). Adolescent chimpanzees increase their signal activity when the
366 mothers of their younger playmates are witnessing the playful session, with facial expressions reaching
367 peak levels of production when the roughness of their play is particularly high. Therefore, it appears
368 evident that adolescent chimpanzees are able to fine-tune their playful facial displays not only to manage
369 the session itself but also to manipulate the social context in which the session occurs in a sort of
370 audience-effect (Flack et al. 2004).

371 In monkeys, the facial expressions are more fixed, whereas in hominoids they may show a
372 gradient of intensity, which appears to be strictly associated with the positive emotions experienced by
373 the subject (Parr 2003). This phylogenetic distinction is supported by the observation that bonobos (like
374 chimpanzees) sometimes exhibit a play face while engaging in solitary play (Palagi 2008, Cordoni and
375 Palagi 2011, Palagi and Cordoni 2012); this is not the case in macaques, capuchins, and marmosets (van
376 Hooff and Preuschoft 2003, de Marco and Visalberghi 2007). Van Hooff and Preuschoft (2003, p. 257)
377 affirmed that this ‘private emotional expression’ may suggest not only a playful intent directed to a
378 potential partner but also a capacity for self-reflection or self-awareness, which are the precursors to
379 more complex forms of cognition in social communication. Recently, Pellis and Pellis (2011)
380 demonstrated that the role of play signals in self-regulating emotional state is also present in spider
381 monkeys (*Ateles geoffroyi*). In this primate species head shaking functions to facilitate amicable social
382 contacts and occurs frequently during juvenile RT. Yet, juveniles also shake their heads during solitary-

383 locomotor play. Pellis and Pellis (2011) tested three different hypotheses to account for headshakes
384 occurring in a solitary context: i) the experience of the unexpected hypothesis, ii) the immature
385 misdirection of signals hypothesis, iii) the *whistling past the graveyard* hypothesis. The play as "the
386 experience of the unexpected hypothesis" was found wanting because solitary headshakes were most
387 frequent in early infancy, before the onset of the juvenile peak in play. The "immature misdirection of
388 signals hypothesis" was also inadequate because the headshakes were correctly directed at conspecifics,
389 but not at inanimate objects that were manipulated and mouthed. Both also failed to predict the
390 occurrence of the observed solitary headshakes in adults. The hypothesis best supported by the data was
391 that of *whistling past the graveyard*, which predicts that, under some situations, headshaking is self-
392 directed to promote action and take heart when confronting contexts of uncertainty. Similarly, a study of
393 the use of the FPF in juvenile Tonkean macaques during social play found that about a third of their
394 occurrences are best accounted for as being performed to regulate the performer's mood (Pellis et al.
395 2011).

396 *Humans.* Charles Darwin, in *The expression of emotions in man and animals* (1872) underlined
397 that human facial expressions have strong similarities with those of other animals. Such similarity
398 represents a shared heritage of our species, which supports the evolutionary continuity between humans
399 and other mammals. According to some, the origin of human facial expressions, such as smiling, dates
400 back to an ancestral nonhuman primate (de Waal 2003, van Hooff and Preuschoft 2003).

401 Smiling and laughing are ubiquitous among humans and pervasive in play interactions. Socially
402 elicited smiling occurs in early infancy (beginning near the end of the first month) and is one of the first
403 signals of positive emotions (for review see Lewis 2000; Messinger et al. 2012). Further, smiling among
404 children and adults happens predominantly in social contexts where the signal can be observed (Bainum
405 et al. 1984, Provine and Fischer 1989).

406 Child ethologists and developmental researchers have long recognized that there are distinct forms
407 and functions of smiling (e.g., Blurton-Jones 1971, McGrew 1972, Cheyne 1976). Cheyne (1976)
408 describes three main types of smiles observed among children: the upper smile, closed smile, and broad
409 smile. The upper smile exposes the upper teeth while covering the lower teeth and is most common in
410 social play and friendly interactions. All the teeth are covered in the closed smile and it is commonly
411 observed in solitary play. The broad smile exposes both upper and lower teeth and characterizes social
412 play; this smile can be phylogenetically related to that of chimpanzees (for review see McGrew 1972
413 and Cheyne 1976) and adult gelada FPF (Palagi and Mancini, 2011). In an observational study of
414 preschool children 2-4 year-olds, Cheyne (1976) found that the upper smile increased in frequency with
415 age, whereas the other two types of smiles remained stable across each age. As social play becomes
416 more prominent so does the upper smile, as the upper smile seems to signal and support social play.

417 Laughter is one of the first social vocalizations that human infants express, typically occurring
418 between three and four months of age in response to social stimulation (Sroufe and Waters 1976, Field
419 1982). Human laughter is characterized by explosive and repetitive sound. Gervais and Wilson (2005)
420 distinguish between two forms of human laughter: “Duchenne (stimulus-driven and emotionally
421 valenced) and non-Duchenne (self-generated and emotionless) laughter” (p. 396) (Figure 1). Duchenne
422 laughter is thought to be involuntary laughter provoked by unexpected incongruities in safe or playful
423 situations or “nonserious social incongruity” (Gervais and Wilson 2005, p. 399). Duchenne human
424 laughter has been described as similar in structure (e.g., Provine 2000, Matsusaka 2004) and in function
425 to the play pants of great apes (Gervais and Wilson 2005). Even though there appears to be a strong
426 biological predisposition for Duchenne laughter (for review see Gervais and Wilson 2005), there is
427 cross-cultural variation in the expression of such laughter (e.g., Weisfeld 1994). Nonetheless, the major

428 provocation of Duchenne laughter – “nonserious social incongruity” – is the same in both humans and
429 apes (for review see Gervais and Wilson 2005).

430 Laughter is notably contagious and social (Provine 2004). Provine and Fischer (1989) found that
431 among college students, laughter was 30 times more likely to occur in social contexts than when they
432 were alone, further supporting the idea that laughter is an important social signal. Furthermore, they
433 found that solitary laughter was remarkably rare and occurred mostly in response to media, which is
434 arguably a vicarious social situation. Gervais and Wilson (2005) have characterized laughter (Duchenne
435 laughter) as an “emotional contagion” (p. 404) not only promoting play but also functioning similarly to
436 social play.

437 Like other great apes, humans not only smile in social contexts but also smile when alone.
438 Fridlund (1991) found that college students who viewed a pleasant video showed solitary smiling and
439 that this smiling was unrelated to their self-reported happiness. Fridlund argued that when alone
440 (without explicit or implicit audiences) the students may have evoked sociality or an imagined audience
441 (e.g., the film may have brought someone they know to mind). Thus, solitary smiling may be indicative
442 of imagining sociality. Similar to smiling, solitary laughter is usually associated with imagined or
443 vicarious social situations such as listening or watching media (Provine 2004). Not surprisingly, solitary
444 smiling and laughter are less common than smiling and laughter in interpersonal contexts. In an
445 observational study of preschool children, Bainum et al. (1984) found that only 5% of smiling and
446 laughter occurred in solitary contexts.

447 In conclusion, the systematic study of primate facial expressions, body postures, and movements
448 during solitary play could provide valuable insights into animal emotion and cognition, further making
449 the behavioral separation between *Homo sapiens* and other mammalian species more subtle. Darwin
450 *docet*.

451 **4. Self-handicapping and role reversals as aspects of communication during RT**

452 Self-handicapping, the ability of animals (including humans) to put themselves into
453 unnecessarily disadvantageous or vulnerable positions or situations (Bekoff 2001a, b; Bauer and Smuts
454 2007) is an interesting and widespread phenomenon that occurs during play. In a restrictive, commonly
455 held view, self-handicapping is typically considered to involve a reduction in the strength and velocity
456 of movements when older animals play with younger ones. However, this view underestimates the
457 variety of different contexts and ways that different species can engage in self-handicapping. For
458 example, a younger partner can engage in self-handicapping as well as its older partner (as occurs
459 among dogs; Bauer and Smuts 2007), and self-handicapping may also occur during solitary play when
460 no partner is present (Palagi, personal observation, Petrů et al., 2008). Self-handicapping can arise as an
461 animal orients its body in an unusual or unnatural position with respect to either its play partner or to the
462 physical environment. Thus, self-handicapping can occur in three ways: social self-handicapping, such
463 as when a stronger partner adopts an inferior posture, kinematic self-handicapping, such as when an
464 animal adopts some physically demanding movements and postures, and sensory self-handicapping,
465 such as when an animal closes its eyes when executing a movement (Petrů et al. 2009). Špinka et al.
466 (2001) argued that self-handicapping movements involving awkward body positions are likely
467 precursors for signals of an individual's playful intention. For example, Burghardt and Burghardt (1972)
468 described a peculiar-back-rolling invitation pattern in bear cubs during play (Fig. 1). Moreover, during
469 social play, bonobos (*Pan paniscus*) like to walk on horizontal branches with their eyes covered, while
470 trying to maintain equilibrium and avoid falling down. During their "blindman's bluff" game, they cover
471 their eyes with large leaves or clothes while trying to catch playmates or to reach something in the
472 environment (Palagi, personal observation). It is therefore clear that the object is deliberately used by
473 individuals to create a novel, self-handicapping situation, which can be perceived by the playmate as a

474 clear signal of benign intent (Figure 1). A similar phenomenon has been also observed in Douc langurs
475 (*Pygathrix nemaeus nemaeus*) (Kavanagh, 1978), Japanese macaques (*Macaca fuscata*) and orangutans
476 (*Pongo pygmaeus*) (Russon and Vasey 2012).

477 Role reversal, which occurs when play partners take turns adopting complementary roles (Altmann
478 1962), is another common feature of RT communication. The "50:50 rule" (Altmann 1962) says that,
479 within pairs, each animal must play the offensive and defensive roles roughly equally in order for play to
480 remain appealing to both partners. This appears to be the case in many instances, such as in juvenile rats
481 (Figure 1). However, the 50:50 rule varies widely, both within and between species (Cordoni and Palagi
482 2011). In young male rhesus monkeys, play-fighting roles tend to be fairly egalitarian at first, but as the
483 partners grow older, one tends to adopt the offensive role more often than the other (Symons 1978).

484 *Rodents.* While some rodent species exhibit high levels of solitary locomotor-rotational (SLR)
485 play that stimulates others to engage in RT (Pellis and Pellis, 1983), others do not. For example, Syrian
486 golden hamsters (*Mesocricetus auratus*) tend to be rather stolid creatures and, unlike rats, they never
487 jump, run or pounce on one another (Pellis and Pellis 1988). However, the complexity of the play is not
488 correlated with the presence of SLR movements – hamsters have complex patterns of playful wrestling
489 as do rats (Pellis and Pellis 1987, 1988), and even though house mice have patterns of SLR play that are
490 as exaggerated as those of rats (van Oortmerssen 1971), their RT is limited to a simple pattern of
491 approach-withdrawal (Pellis and Pasztor 1999). However, mice do show inter-animal coordination in
492 some of their locomotor-rotational play (Terranova et al. 1993, Laviola and Alleva 1995), suggesting
493 that even in a species with rudimentary social play, SLR movements may facilitate social engagement.

494 *Carnivores.* Among carnivores, self-handicapping and role reversals have been systematically
495 studied only in domestic dogs. In a play group of 24 unrelated but familiar adult dogs, Bauer and Smuts
496 (2007) found that in most playing pairs, one dog tended to adopt the offensive role significantly more

497 often than the 50:50 rule would predict. In a subset of pairs in which dominance relations were clear, the
498 more dominant dog was in the winning role significantly more often. The most dominant dog in the
499 group hardly ever relinquished the offensive role during play, but many of the other dogs nevertheless
500 sought her out for play, indicating that frequent role reversals are sometimes less important than other
501 factors in determining play partner preferences. On the other hand, in a few dyads, roles were quite
502 symmetric. This large variation across pairs may be linked to their relationship quality. Those pairs of
503 dogs who are good friends and/or those pairs who live together may develop reciprocal roles in play
504 because their relationships, in general, are more cooperative than those of dogs with more ephemeral
505 relationships. Also contrary to prediction, Bauer and Smuts (2007) found that younger dogs self-
506 handicapped more than their older, more experienced partners did. Since younger dogs in general seem
507 more eager to play than older dogs do, perhaps younger dogs self-handicapped more in order to induce
508 older partners to play. This interpretation is consistent with the fact that younger animals also performed
509 play signals more frequently than did their older partners (Bauer and Smuts 2007). Ward et al. (2008)
510 studied play among puppies within four different litters. They found that puppies developed specific
511 play partner preferences and that these preferences became more marked over time. Similar to adult
512 dogs, young littermate pairs did not tend to follow the 50:50 rule, and their play became even more
513 asymmetric with age (see also McNutt and Boggs 1996 for African wild dogs *Lycaon pictus*).

514 *Nonhuman primates.* Petrù et al. (2009) investigated the actions performed during play in five species of
515 monkeys (*Semnopithecus entellus*, *Erythrocebus patas*, *Chlorocebus pygerythrus*, *Cercopithecus*
516 *neglectus* and *Cercopithecus diana*). Of the 74 patterns characterized, 33 (45%) were judged to have a
517 self-handicapping character. The self-handicapping patterns mostly involved making movements more
518 physically demanding than necessary and exaggerating sensory input such as by performing somersaults
519 and flips. Adult bonobos often engage in solitary energetic play sessions, where subjects challenge

520 themselves in extremely acrobatic performances during which their vestibular apparatus is stimulated
521 vigorously (Palagi and Paoli 2007). At every age, bonobos love to climb, jump, dangle, and pirouette
522 from supports in the environment while rapidly twisting. They often somersault on the ground covering
523 several meters and alternate such performance with short and fast bouts of running (Palagi and Cordoni,
524 2012). Given that imitation can facilitate the social transmission of communicative signals (Miklósi
525 1999), it is possible that the observation of another animal engaged in playful self-handicapping may
526 increase the observer's motivation to play. Palagi (2008) tested the hypothesis of the social function of
527 SLR play in adult bonobos. Bonobos use this communicatory tactic to elicit a playful response in the
528 receiver: with about 50% of the solitary play sessions being followed by RT. Moreover, RT is more
529 frequent when preceded by solitary play than by other self-directed behaviors, with pirouettes and
530 somersaults being particularly frequent in the solitary play sessions directly preceding RT. The capacity
531 of the great apes to create or invent new communicative signals by modifying pre-existing behavioral
532 patterns (ontogenetic ritualization as defined by Tomasello and Call 1997) is probably at the basis of this
533 sophisticated use of solitary play in bonobos. Indeed, sophisticated forms of self-handicapping, such as
534 chasing a partner with the eyes closed occurs more frequently in apes than Old World Monkeys (Russon
535 and Vasey 2012).

536 *Humans.* Children alternate between who is aggressing and who is the victim, with both partners
537 self-handicapping (Pellegrini 2009). For example, the “aggressor” may use exaggerated movements and
538 open-handed hits and the “victim” may slow down to be caught or move into striking distance of the
539 aggressor. In cases of adult-child play or in other unequal partnerships, the larger more competent and
540 stronger partner typically self-handicaps (Pellegrini 2009). Parke and colleagues (1992) suggest that the
541 ability to process signals can be rooted in the RT play occurring during parent-offspring interactions.
542 The amount of time spent in parent-offspring RT is positively correlated with children's ability to

543 translate bodily expressions into emotional states thus, in turn, affecting the length of play sessions
544 (Parke et al. 1992). Moreover, Pellegrini and coworkers (2006) posit that self-handicapping likely
545 enhances the length of play bouts by increasing the players' motivation and deterring boredom. Since
546 RT gives opportunities to practice role reciprocation and self-handicapping, by playing with parents
547 children can acquire an array of social strategies to engage in and maintain social interactions with peers
548 (Pellegrini 1993).

549 Relatively few human studies have specifically focused on self-handicapping, restraint or role
550 reversal (Aldis 1975, Fry 1987, Smith and Boulton 1990, Boulton 1991). Boulton (1991) noted that self-
551 handicapping creates challenges, as it increases the difficulty in detecting whether a child is showing
552 restraint (Fig. 1). However, it seems that the use of self-handicapping during RT can vary with age.
553 Pellegrini (2002) points out that self-handicapping and restraining one's strength is less prominent in
554 adolescence when "cheating" becomes more common. The use of play fighting at this developmental
555 stage can be one pathway to establish dominance relationships.

556 Little is known about human solitary self-handicapping and how this may relate to RT. Boulton
557 (1991) found that same-sex 8- and 11-year-old children in the UK tended to spend time in close
558 proximity prior to engaging in RT. However, whether children displayed self-handicapping prior to RT
559 is not known. Boulton has also noted that children who engage in RT play also tend to spend a lot of
560 time together in other activities. Presumably, engaging in RT and self-handicapping is safer (i.e., less
561 likely to lead to harm or real aggression) if you know your play partner well.

562 **5. Let's share our emotions! Facial and body mimicry during play**

563 Matching one's own behavior with that of others gives an individual the possibility to synchronize
564 their activity with those of group members, to copy their behavior, and to place their behavioral activity
565 in the appropriate context. The context of play, due to its plasticity, safety, and emotional involvement,

566 provides a good substrate to investigate these mimicry processes. Understanding others' emotional states
567 instantly allows an individual to foresee their playmates' intentions (Palagi 2008) and fine-tune their
568 motor sequences accordingly (Provine 1996; Palagi and Mancini 2011). So we can hypothesize that the
569 ability to promptly respond with a mimicked action is an adaptive behavior.

570 *Carnivores* Smuts (2007) argued that animals cooperating with one another in a "real" context
571 (e.g., when resources or status are being contested) might negotiate their alliances first through
572 synchronization of movements, which could occur during greetings, play or other contexts. Many
573 different signals can be exchanged to negotiate cooperation, but they might not be honest. However,
574 precise synchrony between different animals *is* cooperation, unmistakable evidence that two individuals
575 are sufficiently attuned to each other that they can develop a dance-like pattern of interaction that
576 transcends their individuality (Smuts 2007 p. 143). Dog play provides a good example of such
577 synchrony. Although it does not always occur, certain dyads show obvious mimicry and synchrony
578 when they play. This pattern is most striking when dogs synchronize their play bows. During one such
579 bout of play, only 1/30th - 2/30th of a second occurred between the instant the first dog began to lower the
580 forequarters and the instant the second dog began to copy the movement; thus in real time, the bows
581 appeared perfectly synchronous (Smuts, in preparation). Could canine postural mimicry be analogous (at
582 least some of the time) to involuntary rapid facial mimicry in primates (see below)? This possibility
583 deserves attention.

584 *Primates* In primates, different forms of imitation can be distinguished. Some forms are under
585 voluntary and cognitive control, while others are involuntary, more linked to the emotions (Dimberg et
586 al. 2002, Iacoboni 2009). For example, in humans there are two possible responses to positive facial
587 expressions: automatic responses (within 1.0 s) and non-automatic responses (within 5.0 s). Automatic
588 affective laughter has been associated with the spontaneous Duchenne smile (a facial expression

589 involving the contraction of both the zygomatic major and the orbicularis oculi muscles) and non-
590 automatic laughter has been associated with the non-Duchenne smile (involving only the contraction of
591 the zygomatic major muscle, a smile purely controlled and detached from any emotion) (Dimberg et al.
592 2000, Wild et al. 2003). The involuntary, automatic, mirroring and rapid response (e.g. the Duchenne
593 smile, Figure 1) given by the receiver is called Rapid Facial Mimicry (RFM) and can be distinguished
594 from other forms of imitation (Jacoboni 2009) by the rapidity of the matched reply. In humans, other
595 apes, and monkeys, RFM plays an important role in emotional contagion by affecting one another's
596 emotions or state of arousal (Davila Ross et al. 2008, de Waal 2008). There is evidence that facial
597 mimicry in playful contexts correlates with the success of playful interactions. For example in
598 chimpanzees, play bouts last more when the play face is bidirectionally performed by the two players
599 (Waller and Dunbar 2005). Moreover social play sessions characterized by facial replication last longer
600 than those sessions punctuated only by spontaneous laughter (Davila Ross et al. 2011). It seems,
601 therefore, that the emotional synchronization through playful facial mimicry goes hand in hand with the
602 cooperative side of social play. In humans, facial responsiveness requires a mechanism of "redirection of
603 the sender's neural processing and perception toward one interactant and away from others" (Schmidt
604 and Cohn 2001, p. 14). For both sender and receiver, maintaining a social interaction and exchanging
605 facial expressions imply high-energy costs in terms of attentional investment. In this sense the presence
606 of high levels of RFM during a playful interaction is a clear statement of honesty by the two players that
607 can be translated into fair play. Recent observations in geladas seem to support this hypothesis. In this
608 species play duration length goes hand in hand with RFM but not with delayed facial mimicry (Mancini
609 et al. 2013a, b). In this perspective, the rapid and automatic response, more than the delayed response, is
610 an expression of emotional involvement directly linked to the real motivation of the subject to play.
611

612 **6. Make a gesture to tell me something! Gestures as a cognitive breakthrough**

613 *Carnivores* Play signals, such as the canine play bow, may not be observed if the other animal is
614 not oriented toward the signaler. When one dog's attention has shifted away from the partner during a
615 play session, the other dog first tries to get the partner's attention by barking, touching, or moving into
616 the other's visual field (Horowitz 2009). If the attention-getting behaviors do not result in play, the dog
617 will often continue with attempts to get the partner's attention, often by alternating among different
618 attention-getting behaviors. Dogs also tend to use bumping, biting, or pawing behavior when the partner
619 is socially engaged with someone else, as if they recognize the need for an especially salient attention-
620 grabber in this context. Only when a dog has gained the attention of another does she/he direct play bow
621 toward that dog.

622 *Primates* Mounting by Japanese macaques (*Macaca fuscata*) has similarly been found to act as an
623 attention getting device that can then lead to RT (VanderLaan et al. 2012). These findings on dogs and
624 macaques are noteworthy because they reveal that such attention-gaining signals may be prevalent in
625 taxa beyond the great apes and humans in which they are usually studied. The association between play
626 bow and attention-getting behaviors, in particular, strongly suggests that there is a cognitive dimension
627 to the use of these signals (Figure 1). Such attention gaining actions could form the rudimentary
628 substrate on which the brachio-manual gestures of great apes and humans are built.

629 In apes, gestures are narrowly defined as movements of hands, feet, or limbs with communicative
630 function (Pollick and de Waal 2007). One of the reasons to keep gestures apart from other forms of
631 bodily communication (e.g., canine play bow) is that the two are neurologically distinct in both
632 production and perception by others (Rizzolatti et al. 1996). A single brachio-manual gesture may
633 communicate different messages depending on the social context in which the gesture is used
634 (Tomasello et al. 1997). This kind of dissociation between gesture and context has been observed in all

635 great ape species, including humans (Bruner 1975, Call and Tomasello 2007), and in all contexts,
636 including play.

637 Differently from other forms of communication more strictly linked to emotional components (i.e.,
638 vocalizations and facial expressions), gestures are mainly based on cognitive capacities and experience
639 (Figure 1). Some learning processes must be present to develop such a complex way of communication
640 (Call and Tomasello 2007). In the great apes, one of the proposed learning processes determining the
641 improvement of the gestural repertoire of a given species is that of “ontogenetic ritualization”, which is
642 the capacity to create or invent new communicative signals by modifying pre-existing behavioral
643 patterns (Tomasello and Call 1997), so that a non-communicative pattern becomes communicative. An
644 example for clarifying this concept comes from play in chimpanzees. Juveniles of this species may
645 initiate a play bout by slapping a potential playmate. If the receiver realizes that a play interaction often
646 begins with the initiator raising an arm in preparation for slapping, the former may anticipate by
647 responding, even after perceiving the first part of the movement only. By noticing the anticipation of the
648 receiver, the initiator may realize that the arm raising by itself is sufficient to elicit a playful response
649 and thus, at some future encounters, use the same pattern to elicit play (Tomasello 1990). Although most
650 evidence of ontogenetic ritualization is reported for immature subjects, it appears plausible that also
651 adult apes are able to understand the cause-effect of a gesture, anticipate its function and, consequently,
652 use a modified version of that gesture as a communicative signal (Palagi 2008). There has been
653 controversy, in recent literature, about the ontogeny of the intentional gestures of great apes.
654 Although the hypothesis of ontogenetic ritualization was able to account for the data reported in
655 several studies, more recently doubts about it have arisen. Particularly, Genty et al. (2009),
656 comparing several gorilla populations, found no clear support for such hypothesis. Genty and co-
657 workers detected no evidence that subjects had acquired gestures by imitation or other means of

658 social transfer from conspecifics, such as population-specific differences in repertoire. They
659 proposed that gorillas' gestures are species-typical as a result of genetical channelling in
660 development, as with communicative signals of most other animals.

661 Some recent studies demonstrated that apes have the capacity to invent new gestures (Pika et al.
662 2003, 2005; Liebal et al. 2006) that later may spread to the rest of the colony through social learning
663 processes (Whiten 2000). The invention of new gestures has been reported also in some monkey species
664 although these have less cortical control over manual movements than apes have (Perry et al. 2003,
665 Perry and Manson 2003, Laidre 2008).

666 In all ape species a great variety of gestures has been reported both in the wild and in captivity
667 (Hobaiter and Byrne, 2011). The gestural repertoire initially increases with age reaching the climax
668 between the age of three-six years, and decreases again in adulthood (Tomasello et al. 1997, Call and
669 Tomasello 2007; Hobaiter and Byrne, 2011). This bell-shaped distribution of the gestural repertoire
670 can be linked to the fact that it is mainly expressed during social play interactions, whose frequency
671 shows the same age-related, bell-shaped distribution over time (Fagen 1993). Even though few studies
672 have focused on gestural communication in the great apes, all the findings converge on an extensive use
673 of this type of communication during play. The playground could, therefore, be considered as a sort of
674 training ground in which the effectiveness of gestures is tested.

675 Gestural communication during playful interactions seems to be shaped also by the social structure
676 of the species. Hence the highest frequency of gestures has been reported in the playful context in the
677 two *Pan* species (about 55% for bonobos, Pika et al. 2005; 47-70% for chimpanzees, Tomasello et al.
678 1997) that share a fission-fusion social system, characterized by fluid social interactions (Palagi 2006).
679 A slightly lower percentage (about 40%) has been reported for gorillas, which live in a one-male society
680 (Fleagle 1999), where adult relationships are limited to spatial proximity rather than affiliative closeness.

681 The lowest percentage of gestures in the playful context has been observed in orangutans (about 22%)
682 that live in an individual-based fission fusion system (Fleagle 1999, van Schaik 1999). In the two *Pan*
683 species, playful interactions can frequently involve adults, whereas in gorillas and orangutans playful
684 activities are almost exclusively limited to immature subjects (Palagi et al. 2007). Considering the
685 importance of learning in the ontogeny of the gestural repertoire, adult and immature playful contacts
686 appear to be fundamental. Hence, social play in all its forms represents a unique opportunity to train the
687 communicative plasticity that is necessary to acquire the majority of gestures and to use them in an
688 appropriate manner. Even though, we cannot exclude the possibility that some gestures might be also
689 co-opted from other contexts to be used as play signals. Such cognitive plasticity in the use of gestural
690 communication deserves much more attention by scholars of play and intentional communication
691 systems. In fact, understanding the way apes and other primates communicate through gestures and how
692 this capacity develops, becomes central when considering that it has been proposed that our ancestors'
693 first linguistic expressions were in the gestural domain, and not in the vocal domain (Corballis 1999,
694 2002). There are also some neurological findings that support the hypothesis that human language
695 developed from gestural communication (Cantalupo and Hopkins 2001, Kelly et al. 2002; Hopkins et al.
696 2007).

697 As it has been previously discussed, it is during RT interactions that the majority of apes' gestures
698 are performed, so it becomes self-evident that the study of gestural communication during playful
699 activities could help to shed light on the origins of human language.

700

701 **CONCLUSIONS AND FURTHER DIRECTIONS**

702 Play behavior, due to its plasticity and versatility, is a complex phenomenon that challenges not
703 only players but also scholars. By studying play, ethologists, comparative and developmental

704 psychologists, and evolutionary biologists can explore the background on which animal communication
705 has evolved.

706 Many simple and complex signals have been evolved for animals (including humans) to help them
707 to maintain a playful mood and avoid misinterpretation. Most of these signals can have different
708 meanings and roles both during phylogeny and ontogeny. As for ontogeny, the human smile is a
709 particularly illuminating example. During early childhood, infants and toddlers perform almost
710 exclusively the most emotional version of the smile (Duchenne smile), but later, young children,
711 adolescents and adults can enrich their facial communicative repertoire with more cognitive forms of
712 smiles (e.g. non-Duchenne smile) (Gervais and Wilson, 2005).

713 Despite the extreme difficulties related to the issue of animal communication in play, here we
714 attempted a categorization of signals that have been historically considered related to this behavior. First
715 of all, we divided signals according to their specificity. Some signals are based on patterns recruited
716 from other functional contexts (see the left side of Figure 1), others are patterns exclusively designed for
717 play (see the right side of Figure 1) and both these kinds of signals can serve similar functions. This
718 theoretical categorization permits the delineation of, from a functional point of view, a common
719 platform of play communication across different *taxa* thus favoring a comparative approach.

720 The second categorization we introduced was related to the proximate causes that underline the
721 signal itself. Some signals are driven by emotions (lower part of Figure 1) while others by cognition
722 (upper part of Figure 1). Some lineages of animals have exaggerated the inter-play between the
723 emotional and cognitive aspects of play signals, yielding admixtures of communication that have led to
724 very complex forms of RT. For this reason, a clear-cut categorization between emotional and cognitive
725 signals is hard to reach because, to be effectively transmitted, a signal requires the presence of both a
726 sender and a receiver. For example, spontaneous laughter, which is the expression of a positive

727 emotional state, can be read and cognitively utilized by the other playmate to manage and modulate the
728 session. If the laughter occurs during solitary play, the receiver can cognitively interpret the spontaneous,
729 emotion-driven facial expression as a signal indicating the sender's propensity to engage in a social play
730 interaction. In this view, an emotionally driven signal for the sender becomes a cognitive signal for the
731 receiver. The same may apply to self-handicapping and role reversal. They can be considered both
732 intentional communicative signals used strategically by animals to enhance play motivation of
733 conspecifics and a form of emotionally self-rewarding action that can be interpreted by conspecifics as a
734 signal of the benign intent of others.

735 Even though many of these issues have yet to be examined empirically, our review of the play
736 communication literature suggests that a sort of dualism between emotional and cognitive nature of a
737 signal can be detected by applying a "shifting approach". Unveiling the emotional component of a signal
738 can be achieved by accurately analyzing it when the sender is alone (e.g., during solitary play). The
739 morphology (motor action sequence) and the exact time of execution of a signal can be compared and
740 contrasted during either social or solitary play, in order to understand whether the sender's awareness of
741 the presence of an audience (cognitive component) can affect the emission of the signal itself. When the
742 cognitive component comes into play, the signal can be enriched by new elements (exaggeration,
743 amplification, long-lasting performance, repetition) that improve its detection probability by a potential
744 receiver. This approach, whenever performed via standardized and quantitative methods, can be applied
745 both under experimental and naturalistic conditions depending on the species, its social structure,
746 ecological requirements, and psychological complexity.

747 Future studies need to bring together two avenues of investigation. First, as seen from the
748 comparative survey, few species have been studied with the intensity needed to characterize the range
749 and type of play signals used in their repertoire, much less the contexts in which different signals may be

750 used. Given that much of what we know is derived from carnivores, primates and rodents, and that these
751 represent highly diverse taxa, it seems only reasonable to recommend that a broader range of these
752 species be the subject of such a comparative data set. Second, as shown in this review, there is
753 considerable variation across species and lineages of species as to how complex the play can be, and, in
754 part, these variations are likely to depend on the tactics used to ensure that interactions maintain the
755 minimum degree of reciprocity needed for them to remain playful.

756 Aside from these empirical requirements, the emerging comparative data set needs to be integrated
757 with novel theoretical approaches. A deeper understanding about the function of reciprocity in
758 interactions could be provided by mathematical modeling (e.g., game theory, Fagen, 1981; Dugatkin &
759 Bekoff, 2003), which, in turn, could alert researchers to look for variations in behavior that are currently
760 not considered. A better understanding about the range and use of play signals and how these are used to
761 navigate the demands of reciprocation during play could then be used as a basis for analyses involving
762 the methods of comparative biology to determine the factors that have promoted the evolution of signals
763 along the dimensions that we have delineated (Figure 1). Social systems that involve highly nuanced
764 social relationships and expanded cognitive capacity (likely reflected in expansion of frontal areas of the
765 cortex) seem to be promising factors to explore in this regard.

766

767 **ACKNOWLEDGMENTS**

768 Thanks are due to all other participants in the Working Group on Play, Evolution, and Sociality.

769 This research has been supported and funded by National Institute for Mathematical and Biological
770 Synthesis - NIMBioS - (University of Tennessee)

771

772

773 **REFERENCES**

- 774 Aldis O. 1975. *Play fighting*. New York: Academic Press.
- 775 Altmann S. A. 1962. A field study of the sociobiology of rhesus monkeys, *Macaca mulatta*. *Annals of*
776 *the New York Academy of Sciences* 102:338-435
- 777 Armstrong E. 1985. Relative brain size in monkeys and prosimians. *American Journal of Physical*
778 *Anthropology* 66:263–273.
- 779 Bainum C. K., Lounsbury K. R., Pollio H. R. 1984. The Development of laughing and smiling in
780 nursery school children. *Child Development* 55:1946-1957.
- 781 Bauer E. B., Smuts B. B. 2007. Cooperation and competition during dyadic play in domestic dogs,
782 *Canis familiaris*. *Animal Behaviour* 73:489–499.
- 783 Bekoff M. 1974. Social play and play-soliciting by infant canids. *American Zoologist* 14:323–340.
- 784 Bekoff M. 1995. Play signals as punctuation: the structure of social play in canids. *Behaviour* 132:419-
785 429.
- 786 Bekoff M. 2001a. Social play behaviour: cooperation, fairness, trust, and the evolution of morality.
787 *Journal of Consciousness Studies* 8: 81–90.
- 788 Bekoff M. 2001b. The evolution of animal play, emotions, and social morality: on science, theology,
789 spirituality, personhood, and love. *Zygon* 36:615–654.
- 790 Bekoff M., Byers J. A. 1981. A critical reanalysis of the ontogeny and phylogeny of mammalian social
791 and locomotor play. Pages 296–337 in *Behavioral development*, edited by K. Immelmann, G. W.
792 Barlow, L. Petrinovich, Main M. Cambridge: Cambridge University Press.
- 793 Blurton Jones N. 1971. Criteria for use in describing facial expressions of children. *Human Biology*
794 43:365-413.
- 795 Blurton Jones N. 1972. *Ethological studies of child behaviour*. New York: Cambridge University Press.

796 Boulton J. M. 1991. A comparison of structural and contextual features of middle school children's
797 playful and aggressive fighting. *Ethology and Sociobiology* 12: 119-145.

798 Bout N., Thierry B. 2005. Peaceful meaning for the silent bared-teeth displays of mandrills.
799 *International Journal of Primatology* 26:1215–1228.

800 Bruner J. S. 1975. The ontogenesis of speech acts. *Journal of Child Language* 2:1-19.

801 Burgdorf J., Kroes A., Moskal J. R., Pfaus J. G., Brudzynski S. M., Panksepp J. 2008. Ultrasonic
802 vocalizations of rats (*Rattus norvegicus*) during mating, play, and aggression: behavioral
803 concomitants, relationship to reward, and self-administration of playback. *Journal of Comparative*
804 *Psychology* 122:357-367.

805 Burghardt, G. M. 1970. Defining 'communication'. Pages 5-18 in *Communication by chemical signals*
806 edited by J. W. Johnston Jr., D. G. Moulton, A. Turk. New York: Appleton-Century-Crofts.

807 Burghardt G. M. 1973. Instinct and innate behavior: toward an ethological psychology. In J.A. Nevin
808 and G.S. Reynolds (EDS), the Study of Behavior: Learning, motivation, emotion, and instinct. pp
809 322-400. Glenview III: Scott Foresman.

810 Burghardt G. M. 2005. *The genesis of animal play: testing the limits*. Cambridge (MA): MIT Press.

811 Burghardt, G.M. 2011. Defining and recognizing play. Pages 9-18 in *The Oxford handbook of the*
812 *development of play* edited by A. D. Pellegrini. Oxford (UK): Oxford University Press.

813 Burghardt G.M. 2012. The origins, evolution, and interconnections of play and ritual: setting the stage.
814 Pages 34-49 in *Play, Ritual and Belief in animals and in Early Human Societies*. Edited by C.
815 Renfrew, I. Morley, & M. Boyd. Cambridge (UK): John Templeton Foundation.

816 Burghardt G. M., Burghardt L. S. 1972. Notes on the behavioral development of two female black bear
817 cubs: the first eight months. Pages 207-220 in *Bears: their biology and management*, vol. 2, edited by
818 S. M. Herrero. IUCN Publications New Series.

819 Byers J. A. 1984. Play in ungulates. Pages 43-64 in *Play in animals and humans*, edited by P. K. Smith.
820 Oxford (UK): Basil, Blackwell.

821 Call J., Tomasello M. 2007. *The gestural communication of apes and monkeys*. NJ: Lawrence Erlbaum
822 Associates.

823 Cantalupo C., Hopkins W. D. 2001. Asymmetric Broca's area in great apes. *Nature* 414:505.

824 Cheyne J. A. 1976. Development of forms and functions of smiling in preschoolers. *Child Development*
825 47:820-823.

826 Ciani F., Dall'Olio S., Stanyon R., Palagi E. 2012. Social tolerance and adult play in macaque societies:
827 a comparison with different human cultures. *Animal Behaviour* 84:1313-1322.

828 Corballis M. 1999. The gestural origins of language. *American Scientist* 87:138-145.

829 Corballis M. C. 2002. *From hand to mouth: the origins of language*. Princeton (NJ): Princeton
830 University Press.

831 Cordoni G. 2009. Social play in captive wolves: not only an immature affair. *Behaviour* 146:1363-1385.

832 Cordoni G., Palagi E. (2011). Ontogenetic trajectories of chimpanzee social play: similarities with
833 humans. *PLoS ONE* 6(11):e27344. doi:10.1371/journal.pone.0027344.

834 Cullen J. M. 1966. Reduction of ambiguity through ritualization. *Philosophical Transactions of the*
835 *Royal society of London, Series B, Biological Sciences* 251: 363-374.

836 Darwin C. 1872. *The expression of the emotions in man and other animals*. London: John Murray.

837 Davila-Ross M., Allcock B., Thomas C., Bard K. A. 2011. Aping expressions? Chimpanzees produce
838 distinct laugh types when responding to laughter of others. *Emotion* 11:1113-1120.

839 Davila-Ross M., Menzler S., Zimmermann E. 2008. Rapid facial mimicry in orangutan play. *Biology*
840 *Letters* 4:**27-30**.

- 841 De Marco A., Visalberghi E. 2007. Facial displays in young tufted capuchin monkeys (*Cebus apella*):
842 appearance, meaning, context and target. *Folia Primatologica* 78:118-137.
- 843 de Waal F. B. M. 2003. Darwin's legacy and the study of primate visual communication. *Annals of the*
844 *New York Academy of Sciences* 1000:7–31.
- 845 de Waal F. B. M. 2008. Putting the altruism back into altruism: the evolution of empathy. *Annual*
846 *Review of Psychology* 59:279–300.
- 847 Dimberg U., Thunberg M., Elmehed K. 2000. Unconscious facial reactions to emotional facial
848 expressions. *Psychological Science* 11:86-89.
- 849 Dimberg U., Thunberg M., Grunedal S. 2002. Facial reactions to emotional stimuli: automatically
850 controlled emotional responses. *Cognition & Emotion* 16:449–471.
- 851 Donaldson T. M., Newberry R. C., Špinková, M., Cloutier, S. 2002. Effects of early play experience on
852 play behaviour of piglets after weaning. *Applied Animal Behaviour Science* 79:221–231.
- 853 Dugatkin, L. A., Bekoff, M. 2003. Play and the evolution of fairness: a game theory model. *Behavioural*
854 *Processes* 60:209-214.
- 855 Fagen R. 1981. *Animal Play Behavior*. New York: Oxford University.
- 856 Fagen R. 1993. Primate juveniles and primate play. Pages 182–196 in *Juvenile Primates*, edited by M.
857 E. Pereira, L.A. Fairbanks. Chicago (IL): University of Chicago Press.
- 858 Feddersen-Petersen D. 1986. Observations on social play in some species of Canidae. *Zoologischer*
859 *Anzeiger* 217:130-144.
- 860 Feddersen-Petersen D. 1991. The ontogeny of social play and agonistic behaviour in selected canid
861 species. *Bonn. Zool. Beitr.* 42:97-114.

862 Field T. M. 1982. Individual differences in the expressivity of neonates and young infants. Pages 279–
863 295 in *Development of nonverbal behavior in children*, edited by R. Feldman. New York: Springer-
864 Verlag.

865 Flack J. C., Jeannotte L. A., de Waal F. B. M. 2004. Play signaling and the perception of social rules by
866 juvenile chimpanzees (*Pan troglodytes*). *Journal of Comparative Physiology* 118:149–159.

867 Fleagle J. G. 1999. *Primate adaptation and evolution*. Second edition. San Diego:Academic Press.

868 Foroud A., Pellis, S. M. 2002. The development of ‘anchoring’ in the play fighting of rats: Evidence for
869 an adaptive age-reversal in the juvenile phase. *International Journal of Comparative Psychology*
870 15:11-20.

871 Foroud A., Pellis, S. M. 2003. The development of ‘roughness’ in the play fighting of rats: a laban
872 movement analysis perspective. *Developmental Psychobiology* 42:35-43.

873 Fox M. W. 1970. A comparative study of the development of facial expressions in canids: wolf, coyotes
874 and foxes. *Behaviour* 36:49-73.

875 Fridlund A. J. 1991. Sociality of solitary smiles: potentiation by an implicit audience. *Journal of*
876 *Personality and Social Psychology* 60:229-240.

877 Geist V. 1978. On weapons, combat and ecology. Pages 1-30 in *Advances in the Study of*
878 *Communication and Affect, Aggression, Dominance and Individual Spacing*, vol 4, edited by L.
879 Krames, P. Pliner, T. Alloway. New York, NY: Plenum Press.

880 Genty E, Breuer T, Hobaiter C, Byrne RW (2009) Gestural communication of the gorilla (*Gorilla*
881 *gorilla*): repertoire, intentionality and possible origins. *Animal Cognition* 12:527–546.

882 Gervais M., Wilson D. S. 2005. The evolutions and functions of laughter and humor: a synthetic
883 approach. *Quarterly Review of Biology* 80(4):395–430.

884 Graham K.L., Burghardt G.M. 2010. Current perspectives on the biological study of play: signs of
885 progress. *Quarterly Review of Biology* 85(4): 393-418.

886 Handelman, B. 2008, 'Canine Behavior: A Photo Illustrated Handbook' WA: Wolf and Word Press.

887 Hayaki H. 1985. Social play of juvenile and adolescent chimpanzees in the Mahale Mountains National
888 Park, Tanzania. *Primates* 26:343–360.

889 Henry J. D., Herrero, S. M. 1974. Social play in the American black bear: Its similarity to canid social
890 play and an examination of its identifying characteristics. *American Zoologist* 14:371–389

891 Hinde R. A. 1982. *Ethology: Its nature and relations with other sciences*. New York: Oxford University
892 Press.

893 Hobaiter C., Byrne R.W. 2011. The gestural repertoire of the wild chimpanzee. *Animal Cognition*
894 14:745–767.

895 Hopkins W. D., Russell J., Cantalupo C. 2007. Neuroanatomical correlates of handedness for tool use in
896 chimpanzees (*Pan troglodytes*): implication for the evolution of language. *Psychological Science*
897 18:971-977.

898 Horowitz A. 2009. Attention to attention in domestic dog (*Canis familiaris*) dyadic play. *Animal*
899 *Cognition* 12:107-118.

900 Iacoboni M. 2009. *Imitation, empathy, and mirror neurons*. *Annual Review of Psychology* 60:253-260.

901 Jolly A. 1966. *Lemur behaviour: a Madagascar field study*. Chicago: University of Chicago Press.

902 Kavanagh M. 1978. The social behavior of Doucs (*Pygathrix nemaeus nemaeus*) at San Diego Zoo.
903 *Primates* 19(1):101-114.

904 Kelly S. D., Iverson J., Terranova J., Niego J., Hopkins M., Goldsmith L. 2002. Putting language back in
905 the body: speech and gesture on three timeframes. *Developmental Neuropsychology* 22:323–49.

906 Knutson B. Burgdorf J., Panksepp J. 1998. Anticipation of play elicits high-frequency ultrasonic
907 vocalizations in young rats. *Journal of Comparative Psychology* 112:65-73.

908 Kuczaj S. A., Horback, K. M. 2013. Play and emotion. Pages 87-111 in *Emotions of Animals and*
909 *Humans: Comparative Perspectives*, edited by S. Watanabe, S. Kuczaj. New York: Springer.

910 Laidre M. E. 2008. Do captive mandrills invent new gestures? *Animal Cognition* 11:179–187.

911 Laviola G., Alleva E. 1995. Siblings effects on the behavior of infant mouse litters (*Mus domesticus*).
912 *Journal of Comparative Psychology* 109:68-75.

913 Lewis M. 2000. The emergence of human emotions. Pages 623-636 *Handbook of emotions*, 2nd edition,
914 edited by M. Lewis, J. M. Haviland-Jones. New York: Guilford.

915 Liebal K., Pika S., Tomasello M. 2006. Gestural communication of orangutans (*Pongo pygmaeus*).
916 *Gesture* 6:1–38.

917 Mancini G., Ferrari P. F., Palagi E. 2013a. In play we trust. Rapid facial mimicry predicts the duration of
918 playful interactions in geladas. *PLoS ONE* 8(6):e66481. doi:10.1371/journal.pone.0066481

919 Mancini G., Ferrari P. F., Palagi E. 2013b. Rapid facial mimicry in geladas. *Scientific Reports* 3:1527-
920 1533.

921 Matsusaka T. 2004. When does play panting occur during social play in wild chimpanzees? *Primates*
922 45:221-229.

923 McFarland D. 1987. *The Oxford companion to animal behaviour*. Oxford (UK): Oxford University
924 Press.

925 McGrew W. C. 1972. *An ethological study of children's behavior*. New York: Academic Press.

926 McNutt J., Boggs L. 1996. *Running wild: dispelling the myths of the african wild dog*. Smithsonian
927 Washington (DC): Institution Press.

- 928 Messinger D. S., Mattson W. I., Mahoor M. H., Cohn J. F. 2012. The eyes have it: making positive
929 expressions more positive and negative expressions more negative. *Emotion* 12:430-436.
- 930 Miklósi A. 1999. The ethological analysis of imitation. *Biological Review* 74:347-374.
- 931 Morris D. 1966. The rigidification of behaviour. *Philosophical Transaction of the Royal Society of*
932 *London Series B, Biological Sciences* 251:327-330.
- 933 Palagi E. 2006. Social play in bonobos (*Pan paniscus*) and chimpanzees (*Pan troglodytes*): implications
934 for natural social systems and interindividual relationships. *American Journal of Physical*
935 *Anthropology* 129: 418-426.
- 936 Palagi E. 2008. Sharing the motivation to play: the use of signals in adult bonobos. *Animal Behaviour*
937 75: 887-896.
- 938 Palagi E. 2009. Adult play fighting and potential role of tail signals in ringtailed lemurs (*Lemur catta*).
939 *Journal of Comparative Psychology* 123: 1-9.
- 940 Palagi E., Antonacci D., Cordoni G. 2007. Fine-tuning of social play in juvenile lowland gorillas
941 (*Gorilla gorilla gorilla*). *Developmental Psychobiology* 49: 433-445.
- 942 Palagi E., Cordoni G. (2012). The right time to happen: play developmental divergence in the two *Pan*
943 species. *PLoS ONE* 7(12):e52767. doi:10.1371/journal.pone.0052767.
- 944 Palagi E., Gregorace A., Borgognini Tarli S. 2002. Development of olfactory behavior in captive ring-
945 tailed lemurs (*Lemur catta*). *International Journal of Primatology* 23:587-599.
- 946 Palagi E., Mancini G. 2011. Playing with the face: playful facial “chattering” and signal modulation in a
947 monkey species (*Theropithecus gelada*). *Journal of Comparative Psychology* 125: 11-21.
- 948 Palagi E., Paoli T. 2007. Play in adult bonobos (*Pan paniscus*): modality and potential meaning.
949 *American Journal of Physical Anthropology* 134:219-225.

- 950 Parke R. D., Cassidy J., Burks V. M., Carson J. L., Boyum L. 1992. Familial contribution to peer
951 competence among young children: the role of interactive and affective processes. Pages 107-134 in
952 *Family-peer relationships: modes of linkage*, edited by R. D.Parke, G. Ladd. Hillsdale (NJ):
953 Erlbaum.
- 954 Parr L. A. 2003. Emotional recognition by chimpanzees. Pages 288-292 in *Animal Social Complexity*,
955 edited by F. B. M. de Waal, P. L. Tyack. Cambridge (MA): Harvard University Press.
- 956 Pellegrini A. D. 1993. Boy's rough and tumble play, social competence, and group composition. *British*
957 *Journal of Developmental Psychology* 11: 237-248.
- 958 Pellegrini A. D. 2002. The development and possible function of rough-and-tumble play. Pages 438-454
959 in *Handbook of social development*, edited by C. H. Hart, P. K. Smith. Oxford: Blackwell.
- 960 Pellegrini A. D. 2009. *The role of play in human development*. New York: Oxford University Press.
- 961 Pellis S. M. 1988. Agonistic versus amicable targets of attack and defense: Consequences for the origin,
962 function and descriptive classification of play-fighting. *Aggressive Behavior* 14:85-104.
- 963 Pellis S. M. 1997. Targets and tactics: the analysis of moment-to-moment decision making in animal
964 combat. *Aggressive Behavior* 23:107-129.
- 965 Pellis S. M., McKenna M. M. 1995. What do rats find rewarding in play fighting? An analysis using
966 drug-induced non-playful partners. *Behavioural Brain Research* 68:65-73.
- 967 Pellis S. M., Pasztor T. J. 1999. The developmental onset of a rudimentary form of play fighting in mice,
968 *Mus musculus*. *Developmental Psychobiology* 34:175-182.
- 969 Pellis S. M., Pellis V. C. 1983. Locomotor-rotational movements in the ontogeny and play of the
970 laboratory rat *Rattus norvegicus*. *Developmental Psychobiology* 16:269-286.
- 971 Pellis S. M., Pellis V. C. 1987. Play-fighting differs from serious fighting in both target of attack and
972 tactics of fighting in the laboratory rat *Rattus norvegicus*. *Aggressive Behavior* 13:227-242.

- 973 Pellis S. M., Pellis V. C. 1988. Play-fighting in the Syrian golden hamster *Mesocricetus auratus*
974 Waterhouse, and its relationship to serious fighting during post-weaning development.
975 *Developmental Psychobiology* 21:323-337.
- 976 Pellis S. M., Pellis V. C. 1996. On knowing it's only play: the role of play signals in play fighting.
977 *Aggression and Violent Behavior* 1: 249–268.
- 978 Pellis S. M., Pellis V. C. 1997. Targets, tactics and the open mouth face during play fighting in three
979 species of primates. *Aggressive Behavior* 23: 41–57.
- 980 Pellis S. M., Pellis V. C. 1998a. The structure-function interface in the analysis of play fighting. Pages
981 115-140 in *Play Behavior: Comparative, Evolutionary, and Ecological Aspects*, edited by M. Bekoff,
982 J. A. Byers. Cambridge (UK): Cambridge University Press.
- 983 Pellis S. M., Pellis V. C. 1998b. The play fighting of rats in comparative perspective: a schema for
984 neurobehavioral analyses. *Neuroscience & Biobehavioral Reviews* 23:87-101.
- 985 Pellis S. M., Pellis V. C. 2009. *The playful brain: venturing to the limits of neuroscience*. Oxford:
986 Oneworld Publications.
- 987 Pellis S. M., Pellis V. C. 2011. To whom the play signal is directed: a study of headshaking in black-
988 handed spider monkeys (*Ateles geoffroyi*). *Journal of Comparative Psychology* 125: 1–10
- 989 Pellis S. M., Pellis V. C., Foroud, A. 2005. Play fighting: Aggression, affiliation and the development of
990 nuanced social skills. Pages 47-62 in *Developmental Origins of Aggression*, edited by R. Tremblay,
991 W. W. Hartup, J. Archer. New York: Guilford Press.
- 992 Pellis S. M., Pellis V. C., Reinhart C. J. 2010. The evolution of social play. Pages 404-431 in *Formative*
993 *Experiences: The Interaction of Caregiving, Culture, and Developmental Psychobiology*, edited by C.
994 Worthman, P. Plotsky, D. Schechter, C. Cummings. Cambridge (UK): Cambridge University Press.

- 995 Pellis S. M., Pellis V. C., Reinhart R. J., Thierry B. 2011. The use of the bared-teeth display during play
996 fighting in Tonkean macaques (*Macaca tonkeana*): sometimes it is all about oneself. *Journal of*
997 *Comparative Psychology* 125:393-403.
- 998 Pellis, S. M. 2002. Keeping in touch: play fighting and social knowledge. Pages 421–427 in *The*
999 *cognitive animal*, edited by M. Bekoff, C. Allen, G. M. Burghardt. Cambridge (MA): MIT Press.
- 1000 Perry S., Manson J. H. 2003. Traditions in monkeys. *Evolutionary Anthropology* 12:71–81.
- 1001 Perry S., Panger M., Rose L., Baker M., Gros-Luis J., Jack K. 2003. Traditions in wild white-faced
1002 capuchin monkeys. Pages 391–425 in *The biology of traditions: models and evidence*, edited by D.
1003 M. Fragaszy, S. Perry. Cambridge (UK): Cambridge University Press.
- 1004 Petit O., Bertrand F., Thierry B. 2008. Social play in crested and Japanese macaques: testing the
1005 covariation hypothesis. *Developmental Psychobiology* 50:399–407.
- 1006 Petrů M., Špinká M., Charvátová V., Lhota S. 2009. Revisiting play elements and self-handicapping in
1007 play: a comparative ethogram of five Old World monkey species. *Journal of Comparative*
1008 *Psychology* 123: 250–263.
- 1009 Petrů M., Špinká M., Lhota S., Šípek P. 2008. Head rotations in the play of Hanuman langurs
1010 (*Semnopithecus entellus*): description and analysis of function. *Journal of Comparative Psychology*
1011 122: 9–18.
- 1012 Pika S., Liebal K., Tomasello M. 2003. Gestural communication in young gorillas (*Gorilla gorilla*):
1013 gestural repertoire, learning, and use. *American Journal of Primatology* 60:95–111
- 1014 Pika S., Liebal K., Tomasello M. 2005. Gestural communication in subadult bonobos (*Pan paniscus*):
1015 repertoire and use. *American Journal of Primatology* 65:39–61.
- 1016 Pollick A. S., de Waal F. B. M. 2007. Ape gestures and language evolution. *Proceedings of the National*
1017 *Academy of Sciences Usa* 104:8184–8189.

- 1018 Poole T. B. 1978. An analysis of social play in polecats (Mustelidae) with comments on the form and
1019 evolutionary history of the open mouth play face. *Animal Behaviour* 26:36-49
- 1020 Power T. G. 2000. Play and exploration in children and animals. Mahwah (NJ): L. Erlbaum.
- 1021 Pozis-Francois O., Zahavi A., Zahavi A. 2004. Social play in Arabian babblers. *Behaviour* 141:425-450.
- 1022 Preuschoft S., van Hooff J. A. R. A. M. 1997. The social function of “smile” and “laughter”: variations
1023 across primate species and societies. Pages 171–189 in *Nonverbal communication: where nature*
1024 *meets culture*, edited by U. Segerstrale, P. Molnár. Mahwah (NJ): Erlbaum.
- 1025 Provine R. R. 2004. Laughing, tickling, and the evolution of speech and self. *Current Directions in*
1026 *Psychological Science* 13:215-218.
- 1027 Provine R. R. 2000. *Laughter: a scientific investigation*. New York: Viking.
- 1028 Provine R. R., Fischer K. R. 1989. Laughing, smiling, and talking: relation to sleeping and social context
1029 in humans. *Ethology* 83:295-305.
- 1030 Provine R.R. 1996. Laughter. *American Scientist* 84:38–45.
- 1031 Rasa O.A.E. 1984. A motivational analysis of object play in juvenile dwarf mongooses (*Helogale*
1032 *undulata rufula*). *Animal Behaviour* 32:579-589.
- 1033 Reinhart C.J., McIntyre D.C., Metz G.A., Pellis S.M. 2006. Play fighting between kindling-prone
1034 (FAST) and kindling-resistant (SLOW) rats. *Journal of Comparative Psychology* 120(1):19-30.
- 1035 Reinhart C. J., Pellis V. C., Thierry B., Gauthier C. A., VanderLaan D. P., Vasey P. L., Pellis S. M.
1036 2010. Targets and tactics of play fighting: competitive *versus* cooperative styles of play in Japanese
1037 and Tonkean macaques. *International Journal of Comparative Psychology* 23:166-200.
- 1038 Rizzolatti G., Fogassi L., Matelli M., Bettinardi V., Perani D., Fazio F. 1996. Localization of grasp
1039 representations in humans by PET:1. Observation versus execution. *Experimental Brain Research*
1040 111:246–252.

- 1041 Russon, A. E., Vasey, P. L. 2012. Eye-covering play in Japanese macaques and orang-utans. Pages 293-
1042 302 in *The Monkeys of Stormy Mountain: 60 years of Primatological Research on the Japanese*
1043 *Macaques of Arashiyama*, edited by J.-B. Leca, M. A. Huffman and P. L. Vasey. Cambridge:
1044 University of Cambridge Press.
- 1045 Schaller G. B. 1972. *The Serengeti lion*. Chicago: University of Chicago Press.
- 1046 Schmidt K. L., J. F. Cohn 2001. Human facial expressions as adaptations: evolutionary questions in
1047 facial expression research. *Yearbook of Physical Anthropology* 44:3-24.
- 1048 Siviy, S. M., Panksepp, J. 1987. Sensory modulation of juvenile play in rats. *Developmental*
1049 *Psychobiology* 20:39-55.
- 1050 Smith P. K., Boulton M. J. 1990. Rough-and-tumble play, aggression and dominance: Perception and
1051 behavior in children's encounters. *Human Development* 33: 271-282.
- 1052 Smuts B. B. 2007. Embodied communication in nonhuman animals. Page 11 in *Human Development in*
1053 *the 21st Century: Visionary Policy Ideas from Systems Scientists*, edited by A. Fogel, B. King, S.
1054 Shanker Oxford: Oxford University press.
- 1055 Špinko M., Newberry R. C., Bekoff M. 2001. Mammalian play: training for the unexpected. *Quarterly*
1056 *Review of Biology* 76: 141–168.
- 1057 Sroufe L. A., Waters E. 1976. The ontogenesis of smiling and laughter: a perspective on the
1058 organization of development in infancy. *Psychological Review* 83:173-189.
- 1059 Stahler D. R., Smith D. W., Landis R. 2002. The acceptance of a new breeding male into a wild wolf
1060 pack. *Canadian Journal of Zoology* 80:360-365.
- 1061 Symons D. 1978. *Play and aggression: a study of Rhesus monkeys*. NY: Columbia University Press.
- 1062 Tattersall I. 1982. *The primates of Madagascar*. New York: Columbia University Press.

1063 Terranova M. L., Laviola G., Alleva E. 1993. Ontogeny of amicable social behavior in the mouse:
1064 Gender differences and ongoing isolation outcomes. *Developmental Psychobiology* 26:467-481.

1065 Thierry B. 2000. Covariation and conflict management patterns across macaque species. Pages 106-128
1066 in *Natural Conflict Resolution*, edited by F. Aureli, F. B. M. de Waal. Berkeley (CA, USA):
1067 University of California Press.

1068 Thierry B., Demaria C., Preuschoft S., Desportes C. 1989. Structural convergence between silent bared-
1069 teeth display and relaxed open-mouth display in the Tonkean macaque (*Macaca tonkeana*). *Folia*
1070 *Primatologica* 52:178–184.

1071 Thompson K. V. 1998. Self assessment in juvenile play. Pages 183-204 in *Animal Play: Evolutionary,*
1072 *Comparative, and Ecological Perspectives*, edited by M. Bekoff, J. A. Byers. Cambridge
1073 (UK):Cambridge University Press.

1074 Thorpe W. H. 1966. Ritualization in ontogeny. *Philosophical Transactions of the Royal society of*
1075 *London, Series B, Biological Sciences* 251: 311-319.

1076 Tomasello M. 1990. Cultural transmission in the tool use and communicatory signaling of chimpanzees?
1077 Pages 274-311 in *"Language" and intelligence in monkeys and apes*, edited by S. T. Parker, K. R.
1078 Gibson. Cambridge: Cambridge University Press.

1079 Tomasello M., Call J. 1997. *Primate Cognition*. Oxford: Oxford University Press.

1080 Tomasello M., Call J., Warren J., Frost G. T., Carpenter M., Nagell K. 1997. The ontogeny of
1081 chimpanzee gestural signals: a comparison across groups and generations. *Evolution of*
1082 *Communication* 1:223–259.

1083 VanderLaan, D. P., Pellis, S. M., Vasey, P. L. 2012. A theoretical model of the development and
1084 evolution of non-conceptive mounting behaviour in Japanese macaques. Pages 186-203 in *The*
1085 *Monkeys of Stormy Mountain: 60 years of Primatological Research on the Japanese Macaques of*

1086 *Arashiyama*, edited by J.-B. Leca, M. A. Huffman and P. L. Vasey. Cambridge: University of
1087 Cambridge Press.

1088 van Hooff J. A. R. A. M. 1989. Laughter and humor, and the “duo-induo” of nature and culture. Pages
1089 120–149 in *The nature of culture*, edited by A. K. Walter. Bochum (D): Brockmeyer.

1090 van Hooff J. A. R. A. M., Preuschoft S. 2003. Laughter and smiling: the intertwining of nature and
1091 culture. Pages 260–287 in *Animal social complexity*, edited by F. B. M. de Waal, P. L. Tyack.
1092 Cambridge (MA): Harvard University Press.

1093 van Lawick-Goodall J. 1968. The behavior of free living chimpanzees in the Gombe Stream Reserve.
1094 *Animal Behaviour Monography* 1:161–311.

1095 van Oortmerssen G. A. 1971. Biological significance, genetics, and evolutionary origin of variability in
1096 behavior within and between inbred strains of mice (*Mus musculus*). *Behaviour* 38:1-91.

1097 van Schaik C.P. 1999. Fission-fusion sociality in Sumatran orang-utans. *Primates* 40:73–90.

1098 Waller B. W., Dunbar, R. I. M. 2005. Differential behavioural effects of silent bared teeth display and
1099 relaxed open mouth display in chimpanzees (*Pan troglodytes*). *Ethology* 111:129-142.

1100 Ward C., Bauer E. B., Smuts B. B. 2008. Partner preferences and asymmetries in social play among
1101 domestic dog, *Canis lupus familiaris*, littermates. *Animal Behaviour* 76:1187-1199.

1102 Way J. G. 2007. Social and play behavior in a wild Eastern coyote, *Canis latrans*, pack. *Canadian*
1103 *Field-Naturalist* 121:397-401.

1104 Weisfeld G. E. 1994. The adaptive value of humor and laughter. *Ethology and Sociobiology* 14:141-169.

1105 Whiten A. 2000. Social complexity and social intelligence. Pages 185–196 in *The nature of intelligence*,
1106 vol. 233, edited by G. R. Bock, J. A. Goode, K. Chichester (UK): Wiley.

- 1107 Wild B., Erb M., Eyb M., Bartels M., Grodd W. 2003. Why are smiles contagious? An fMRI study of
1108 the interaction between perception of facial affect and facial movements. *Psychiatry Research-*
1109 *Neuroimaging* 123:17–36.
- 1110 Wilson S. 1973. The development of social behaviour in the vole (*Microtus agrestis*). *Zoological*
1111 *Journal of the Linnean Society* 52:45-62.
- 1112 Wilson S. C., Kleiman D. G. 1974. Eliciting play: a comparative study. *American Zoologist* 14:341–370.
- 1113 Zahavi A. 1979. Ritualization and the evolution of movement signals. *Behaviour* 72:77–81.

1114

1115 **Figure legend**

1116 The figure shows the categorization of communicative signals commonly used in Rough-and-
1117 Tumble play. The figure is organized according to two theoretical dimensions: signal specificity (signals
1118 designed for play - right side - and signals recruited from other functional contexts - left side) and
1119 proximate causes of signals (emotionally driven signals - upper part - and cognitively driven signals -
1120 lower part).

Table 1. Categorization of communicative signals commonly used in rough-and-tumble play

INTENTIONAL SIGNALS		
PATTERNS RECRUITED FROM OTHER CONTEXTS	<p>FACIAL EXPRESSIONS Non-human primates: lip-smacking (macaques, baboons, geladas), bared teeth (macaques) Humans: non-Duchenne smile</p> <p>BEHAVIOURAL PATTERNS RECRUITED FROM OTHER CONTEXTS AND USED IN ROLE REVERSAL and SELF-HANDICAPPING Carnivores: inhibited bites (dogs, bears, hyenas) and clawing (black bears)</p> <p>Non-human primates: inhibited play fighting (biting, pushing, pulling, slapping, stamping, kicking, etc.) Human children: hitting, kicking, trying to strike another child without contact Rodents: supine position, a typical submissive pattern performed to self-handicap (rats). After knocking the partner to the ground, the 'winner' ceases all movement, stands on all four feet, cocks the head to one side, partially closes the eyes and waits (degus)</p> <p>BEHAVIOURAL PATTERNS RECRUITED FROM OTHER CONTEXTS USED TO SOLICIT PLAY Carnivores: flipping over onto playmate's back in what is best described as an off-balance, head-first somersault (black bears) Primates: anointing the tail in front of the playmate (tail play in ringtailed lemurs) Great apes and humans: brachio-manual gestures</p> <p>BODY POSTURES AND MOVEMENTS Canids: play rolling and squirming during solitary play</p>	<p>FACIAL EXPRESSIONS Non-human primates: full play face in adult geladas during social play. Play faces in juvenile chimpanzees in presence of a particular audience (e.g. the mother of the younger playmate)</p> <p>SELF-HANDICAPPING Human and non-human primates: self-handicapping with objects in great apes and humans (Blindman's bluff game), self-handicapping by closing the eyes in Douc langurs and macaques</p> <p>BODY POSTURES AND MOVEMENTS EXCLUSIVE OF PLAYFUL CONTEXT Canids: play bow</p> <p>Rodents and primates: locomotor-rotational movements during social context Primates: head rotation in social play (langurs) Primates: tickling as an intentional tactile signal (great apes and humans) Many mammalian species: play gallop</p>
		<p>FACIAL EXPRESSIONS Non-human primates: playful facial displays performed in the middle of a social playful session Great apes: playful facial display during solitary play and laughter in early infants (1–6 months) when tickled by the mothers Humans: Duchenne smile, laughter. Laughter represents a preadaptation that, through both biological and cultural evolution, has been gradually elaborated and co-opted to serve new functions in different contexts (non-Duchenne smile, see upper-left quadrant)</p> <p>BODY POSTURES AND MOVEMENTS Rodents and primates: locomotor-rotational movements during solitary play Primates: head rotation in langur solitary play</p>
		<p>EMOTIONAL SIGNALS</p>
		PATTERNS EXCLUSIVE TO PLAY