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

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ABSTRACT

Rough-and-tumble play (RT) is a widespread phenomenon in mammals. Since it involves competition, whereby one animal attempts to gain advantage over another, RT runs the risk of escalation to serious fighting. Competition is typically curtailed by some degree of cooperation and different signals help negotiate potential mishaps during RT. This review provides a framework for such signals, showing that they range along two dimensions: one from signals borrowed from other functional contexts to ones that are unique to play, and the other from purely emotional expressions to highly cognitive (intentional) constructions. Some animal taxa have exaggerated the emotional and cognitive inter-play aspects of play signals, yielding admixtures of communication that have led to complex forms of RT. This complexity has been further exaggerated in some lineages by the development of specific novel gestures that can be used to negotiate playful mood and entice reluctant partners. Play-derived gestures may provide new mechanisms by which more sophisticated communication forms can evolve. Therefore, RT and playful communication provide a window into the study of social cognition, emotional regulation and the evolution of communicative systems.

Key words: Intentional signals; emotional signals; gestures; facial expressions; self-handicapping behavior

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I. INTRODUCTION

Defining play is a difficult matter. Compared to so-called "serious" behaviors, whose functions are more readily discerned, play remains an intriguing challenge. Burghardt (2005, 2011) developed five criteria with which to identify play. (1) Play is not completely functional in the form or context in which it is performed because it does not seem to contribute to current survival. (2) Play is spontaneous, voluntary, intentional, pleasurable, rewarding, reinforcing, or autotelic ("done for its own sake"). (3) Compared to other ethotypic behaviors, play is incomplete, exaggerated, awkward, or precocious and it generally involves patterns modified in their form, sequencing, or targeting. (4) During a play session, the behavioral pattern is performed repeatedly but not in a manner that is rigidly stereotyped. (5) Play is initiated when animals are relatively free from environmental and social stressors.

Beyond its definition, among all social activities, social play stands out for its versatility, plasticity, and unpredictability (Fagen, 1993; Špinka, Newberry, & Bekoff, 2001; Burghardt, 2005, 2012; Palagi, Antonacci, & Cordoni, 2007). Nonetheless, social play does follow rules that, if violated, can lead to serious aggression (Pellis & Pellis, 1998a; Pellis, Pellis, & Reinhart, 2010). While rules are followed in both free play (e.g., play fighting) and structured games (e.g., rugby matches), the nature of the rules differs (Power, 2000; Burghardt, 2005). Structured games, unlike free play, are built on *a priori* rules and the participants have to follow these rules to avoid being penalized. In "free play" the rules to be followed are created by the players. Depending on the players involved (gender, rank, age, size, kin) and the kind of play performed (tickling, locomotor-rotational activities, fighting), each new play session requires the application of 'flexible rules' that can be continually redefined (Pellegrini, 2009). Also, unlike structured games where the rules may be enforced by a third party (e.g., umpire), during free play enforcement of the rules is by the players themselves. These rules could be grounded in affective (e.g., emotional synchrony) or cognitive domains (e.g., intentionality), or some combination of both (Demuru, Ferrari, & Palagi, 2014). Therefore, managing new playful interactions requires sophisticated communicative skills. Social play can also involve considerable communicative effort, improvisation, strategic timing, and creativity. Thus, play may be more mentally demanding than most other non-aggressive behaviors. Indeed, comparative studies of primates have shown that those species that engage in more social play, but not in non-social play, have an enlargement of several brain areas involved in regulating play (Graham & Burghardt, 2010). Because of these demands on flexibility and improvisation during social play, this behavior has been hypothesized to be the engine of much behavioral innovation (Fagen, 1993). We suggest that it is also the reason why social play is an ideal context to study communication and cognition.

II. WHY COMMUNICATION IS FUNDAMENTAL FOR ROUGH-AND-TUMBLE (RT) PLAY

Social play, especially rough-and-tumble play (RT), is intimately associated with communication. Play communication may be among the most complex communication system seen in humans and non-humans. In its most elemental form, communication can be characterized as a behavior that is performed for the advantage of the signaler (Burghardt, 1970). The prolonged reciprocal interactions that occur during play involve a situation in which the players are, often simultaneously, both signalers and receivers.

Despite its seemingly free-flowing appearance, RT can be quite a complex form of social play, because it involves physical contact between partners and may include patterns typical of real fighting. Although there are rules of interaction that distinguish RT from its serious counterparts (Pellis *et al.*, 2010), ambiguous situations arise, such as a playful attack that occurs unexpectedly. In such cases, additional information, such as that provided by particular signals, are important (Aldis, 1975). Although not invariably unambiguous themselves (Pellis & Pellis, 1996, 1997), in many circumstances, these signals can reduce the uncertainty arising from contact during play (Palagi, 2008, 2009). Specific actions, gestures, gaits, vocalizations, facial expressions, and even odors may communicate the playfulness of a potentially dangerous act (Fagen, 1981; Bekoff, 2001a; Palagi, 2006). Signals can help to avoid escalation to real aggression and may prolong play (Burghardt, 2005; Waller & Dunbar, 2005; Mancini, Ferrari, & Palagi, 2013a). Bekoff (1995) stressed the importance of play signals as "punctuation" during playful interactions, especially when play includes elements of hostility**.** Moreover, communicative signals can also have a major role in expressing positive emotions, making the session pleasurable and rewarding for the players (Kuczaj & Horback, 2013). Managing a playful interaction successfully can favor the development of cooperation beyond the play session itself (Palagi & Cordoni, 2012).

RT uses movements, postures and signals recruited from other functional behaviors (e.g., predatory, antipredatory, mating, intra-species agonism) (Bekoff & Byers, 1981; Fagen, 1981, 1993; Pellis, 1988). Some of the gestures used in RT are unique to play (Petrů, Špinka, Charvátová, & Lhota, 2009). Distinguishing between those gestures that are unique and those that are derived from other contexts is often not easy to make for a specific behavioral pattern as making this distinction depends on the thoroughness of the knowledge on the behavioral repertoire of the species being considered. For some species, the repertoire is known sufficiently well to sometimes be able to make this distinction. Chasing-pouncing and lip-smacking are examples of patterns recruited from other functional contexts such as aggression and grooming, respectively. Play bows (Bekoff, 1995), head rotation (Petrů *et al.*, 2009), tickling (van Lawick-Goodall, 1968), vocalizations (Rasa, 1984) and some versions of play faces (Pellis & Pellis, 1997; Palagi, 2008) are patterns that seem to be unique to play (Table 1).

Communication during RT can also vary along another dimension. At one extreme are behaviors such as those facial expressions that are not influenced by the audience and so appear to be primarily determined by the emotional state of the performer (emotional signals) (Cordoni & Palagi, 2011; Pellis, Pellis, Reinhart, & Thierry, 2011). At the other extreme are audience-dependent signals directly targeted to a particular recipient or specific audience (intentional signals), which appear to be produced so as to influence their potential partners' playful behavior (Hobaiter & Byrne, 2011a). Some authors argue that intentionality and emotionality are not mutually exclusive in the signal production process but, rather, may represent two mechanisms that interact during signal production (Liebal, Waller, Burrows & Slocombe, 2014; Demuru et al., 2014). Indeed, some of the signals used during RT fall in between these extremes (Table 1).

This framework is useful because it includes many different kinds of signals that communicate play. Some of these signals, such as the relaxed open mouth, have ancient evolutionary roots and are, therefore, shared among many species. Others, such as play solicitation signals, are highly variable across species, so that particular variants are limited to specific lineages that take highly variable forms across different species.

Although RT has been described in many eutherian and marsupial mammals as well as in some other vertebrates, including birds and frogs (Burghardt, 2005), here we focus on the extensive research available on the most commonly studied mammalian taxa: rodents, carnivores, non-human primates, and humans.

III. RT COMMUNICATION PATTERNS RECRUITED FROM OTHER FUNCTIONAL BEHAVIORS

The incorporation and elaboration of communication signals across functional behavior systems, termed ritualization, is well known in the contexts of feeding, courtship, agonism and parent-offspring interactions (Cullen, 1966; Thorpe, 1966; Burghardt, 1973; Foster, 1995). That play not only recruits ritualized behavior, but may also be the source for new ritualized behavior has not been sufficiently recognized (Burghardt, 2012).

During serious fighting, animals use tactics of attack to deliver blows or bites and tactics of defense to block those strikes. Attacking animals face the threat of retaliation, as a successful parry can be followed by a counterattack by the original defender (Geist, 1978). To attack effectively while minimizing the likelihood of retaliation, offensive maneuvers frequently incorporate a defensive component (Pellis, 1997). The situation is different in RT, that to remain playful it has to be reciprocal (Altmann, 1962; Dugatkin & Bekoff, 2003). During RT animals' maneuvers often work to facilitate role reversals (i.e., successful counterattacks), by either not incorporating defensive actions during attacks (Pellis & Pellis, 1998a), or by not capitalizing on the advantage that has been gained (Pellis *et al*., 2010).

Rodents. RT has been reported in a wide range of rodents (for reviews see Fagen, 1981; Pellis & Pellis, 2009), an order that encompasses some 40% of all mammals (Nowak, 1999). A survey of RT in this order highlights several important lessons that need to be investigated in greater depth across more lineages of mammals (Pellis & Iwaniuk, 2004). First, it shows that the targets being competed over can be derived from functional contexts associated with aggression, predation, sex and other forms of amicable contact (e.g., greeting, grooming). Moreover, there are identifiable phylogenetic trends; the RT of most species of murid rodents thus far studied involves sexual targets, whereas in the other major branches of the order, the sciurids and hystricognaths, there are sub-lineages that compete solely over sexual targets or aggressive targets, and some do both. Second, not all members of this order engage in play fighting (e.g., Happold, 1976), and for those that do, there are gradations of complexity. This can range from playfully pouncing on and contacting the play target, but without the recipient responding (Wilson, 1973), to attacking the target with vigorous defense that involves extensive wrestling (Goldman & Swanson, 1975). In between, there is attack with the defense limited to fleeing (Wolff, 1981). Even among species that have complex wrestling, there can be considerable variation in the frequency with which the most complex form of wrestling play occurs (Pellis, Pellis & Dewsbury, 1989). Third, irrespective of the source of the target competed over during RT, the animals engage in play in manner that increases the likelihood of role reversals (Pellis, Pellis & Foroud, 2005; Pellis et al., 2010), so increasing the likelihood that RT remain playful and does not escalate into aggression (Bekoff, 2001a, b). The extensive experimental work on rats, in particular, has also begun to reveal how multiple levels of neural control mechanisms may been added over evolutionary time in some lineages (Pellis & Iwaniuk, 2004; Pellis & Pellis, 2009). These insights into the neurobiology of RT may also provide a framework for understanding how more cognitively sophisticated signaling systems used in the play of some animals (Table 1) may have evolved.

Most of what has been learned about the neurobiology of RT (Cheng, Taravosh-Lahn & Delville, 2008; Siviy & Panksepp, 2011; Vanderschuren, Niesink & Van Ree, 1997) and the roles that RT has in shaping the development of the brain and social skills (Pellis & Pellis, 2009; Vanderschuren & Trezza, 2014; Wommack, Taravosh-Lahn, David & Delville, 2003), has come from the study of two species, the rat (*Rattus norvegicus*) and the Syrian golden hamster (*Mesocricetus auratus*). With regard to play signals, there has been less intensive work on these species, but there are some such potential signals in rats, that could open the way to test some of the hypotheses generated here.

During RT, rats attack and defend the nape of the neck, which if contacted is nuzzled with the snout (Pellis & Pellis, 1987; Siviy & Panksepp, 1987), whereas during serious fighting, biting attacks are directed at the rump and lower flanks and the face (Blanchard & Blanchard, 1977). Nape attack during RT in rats is blocked by the use of a variety of defensive tactics, with the most common in the juvenile period being to roll over to supine, which leads to the attacker standing over the supine partner (i.e., pin configuration). From this position, they continue to compete for access to their partner's nape

(Panksepp, 1981; Pellis & Pellis, 1987). Rats that have been decorticated at birth grow into juveniles and young adults that are able to engage their peers in RT (Panksepp, Normansell, Cox & Siviy, 1994; Pellis, Pellis & Whishaw, 1992). Most critically, RT of the decorticate rats has the same reciprocal character as RT involving intact rats, suggesting that the ability to follow the rules that keep RT playful involves mechanisms that reside deeper in the brain (Pellis et al., 2010). That is, higher-level cognitive functions that require the cortex (Kolb & Whishaw, 2009) are not needed for complex RT.

The experience of RT in the juvenile period enhances the development of executive functions that includes impulse control (Baarendse, Counotte, O'Donnell & Vanderschuren, 2013) - the ability to 'think before you act' that may be necessary in rough play. The way that juvenile RT experience may do so is by modifying the prefrontal cortex, the area of the cortex associated with executive functions (Vanderschuren & Trezza, 2014). As already noted, RT between pairs of juvenile rats can proceed in a seemingly normal manner in the absence of the entire cortex. However, RT becomes more complex as rats become young adults, when males use a rougher version of RT as a tool for negotiating dominance relationships (Pellis, Hastings, Shimizu, Kamitakahara, Komorowska, Forgie & Kolb, 2005). Adult rats are able to modify the roughness of their play depending on the identity of their partner and on the partner's movements: an ability that is abolished by lesions of the prefrontal cortex (Bell, McCaffrey, Forgie, Kolb & Pellis, 2009; Pellis et al., 2006). This suggests that the cortex, especially the prefrontal cortex, may be critically important when RT occurs in more ambiguous situations (e.g., between partners that differ in size or status, when multiple partners are involved). That is, while the basic skills needed to engage in RT do not require sophisticated cognitive functions, RT can occur in situations in which more sophisticated processing needs to be deployed.

In rodents, the role of postural and movement-related facilitators of play is probably greater than in lineages with a richer repertoire of specific play signals (such as the carnivores and primates discussed below). Thus, in rats, the fighting movements performed during play incorporate self-handicapping postures (Table 1). Nonetheless, experimental findings in rats with damage to the prefrontal cortex show that, in some situations, these play facilitating maneuvers may require the involvement of more sophisticated cognitive processing. Given that the prefrontal cortex is involved in a range of executive functions, with particular sub-regions dealing with particular aspects of decision making (Euston, Gruber & McNaughton, 2012), and that, in some situations, RT can proceed relatively normally in the absence of such cortical mechanisms (Panksepp et al., 1994; Pellis et al., 1992), it suggests that such executive functions preceded the evolution of play, the core circuitry for which involves subcortical mechanisms (Panksepp, 1998; Siviy & Panksepp, 2011; Vanderschuren et al., 1997). For some lineages, where RT has become more complex or has been usurped for novel functions, such as negotiating social relationships (Palagi, 2006; Pellis, 2002), the prefrontal mechanisms may have been co-opted for a more critical involvement in RT.

Unfortunately, as noted above, there are few candidate signals for use in RT by rodents, and those that have been identified have yet to be fully investigated. Conversely, as shown in the proceeding sections, many more, and better studied, examples of play signals are available from other mammalian orders, but much less experimental work on the mechanisms involved is available in these non-rodent species. Therefore, while experimental studies on rats can provide clues as to how play signaling may have evolved increasingly sophisticated neural control, descriptive studies afforded by dogs, monkeys and apes, provide an appreciation for the potential range and complexity of play signals. Such an appreciation can then lead to research questions that may be experimentally tested with rats. As will be explored further below, vocalizations emitted during the RT of rats (Panksepp & Burgdorff, 2003) may provide the kinds of signals that span the range of complexity of play signals suggested in this paper (Table 1).

Carnivores. Domestic dog RT involves several different types of movements (Bauer & Smuts, 2007; Handelman, 2008), which are not strict categories, since elements from any one type may be included in or interspersed with other types. RT among adult wolves has not been systematically described, but it appears to involve all of the play behaviors shown by dogs and, probably, a few others (Cordoni, 2009). In wolves, the first four-six weeks of life are characterized by high frequencies of games involving mimicking, during which the two cubs imitate each other's facial expressions (muzzle-wrinkling, lip-retraction) without being in physical contact (Feddersen-Petersen, 1991). In contrast to wolves, for poodles, games in which they mimic one another mainly involve playful communication in the acoustic modality (e.g. bark games). This form of acoustic play reaches its peak during the fourth month of life (Feddersen-Petersen, 1991).

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

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

Nonhuman primates. Given that primates vary greatly in social systems, rate of development and other socioecological factors (Nowak, 1999), this taxon provides the opportunity to gain a comprehensive understanding of the roles of play communication and the cognitive skills required supporting such communication (Armstrong, 1985). For example, lemurs are relatively small brained, form an independent primate radiation and are more similar to ancestral group-living primates than the more intensively studied monkeys and apes (Tattersall, 1982). The ringtail lemur (*Lemur catta*) is a diurnal and highly terrestrial species, which forms multimale/multifemale social groups characterized by female dominance and male dispersal. The white and black tail of this species is used to communicate and regulate many aspects of social life. The "stink fights" engaged in by males during their agonistic interactions are the most striking example (Jolly, 1966). Males place their tails between the legs and upward in front of the torso and anoint them with the secretion produced by specialized antebrachial glands on wrist and forearm (*anoint-tail)*. Then, the animal may repeatedly flick the tail downward over the top of its head to spread the odor secretion (*wave-tail*). During the agonistic wave-tail pattern, with his ears flattened against the top of his head, the male faces and gazes at the opponent. Mature males also anoint and wave their tails toward females as signals of appeasement or even submission during courtship (solicitation of copulation; Jolly, 1966). There is also a playful version of the communication pattern involving tail use (Jolly, 1966): a good example of a pattern recruited from other functional contexts to communicate during play.

During RT, ringtailed lemurs anoint their tails neither facing the playmate nor even gazing at the playmate (tail-play). Infants begin to perform tail-play during the weaning period (6 months; Palagi, Gregorace, & Borgognini Tarli, 2002). Analysis of the dynamics of RT in juvenile ringtail lemurs indicates that such play resembles real aggression (Pellis & Pellis, 1997). In a number of species, adult RT has been reported to be rougher, having a greater likelihood of escalation into serious fighting (Fagen, 1981; Pellis, 2002; Palagi & Cordoni, 2012). However, the low levels of escalation found in lemurs (Palagi, 2009) suggest that they are able to cope with possible ambiguous situations, with tail-play probably having a role. During play, males generally direct tail-play mostly toward females, which can be very aggressive toward them (Jolly, 1966). Hence, playing with females may be particularly risky for males, who need to clearly signal their own "playful intentions" to avoid misinterpretation. Ringtailed lemurs also frequently use tail-play when playing with less-familiar group members (as determined by low grooming rates). When play occurs between potentially dangerous partners, RT is often characterized by a redundancy of signals (Bekoff, 1974; Henry & Herrero, 1974; Power, 2000). In fact, RT between two individuals, which socially interact at a very low frequency, may be particularly unsafe due to the limited information (physical strength, self-handicapping skill, and movement rapidity) they have about each other.

Humans. In humans, structural descriptions of play have focused on three main characteristics: exaggeration, sequence variability and incompleteness (Pellegrini, 2009). Specific body movements alone, like running and jumping, are not necessarily indicative of play. Instead, play movements are recognized when associated with a constellation of features; for example, exhibiting a play face while jumping on one leg, balancing, swinging, sliding, running in an exaggerated manner or running with a variable sequence (e.g., zig-zagging). Incomplete body movements, like punching near a play partner's arm but not actually making contact, are also used as communication during play. Blurton Jones (1972), in an observational study of 2- and 4-year-olds, found in a factor analysis that the RT play factor had high loadings for laughing-play face, run, jump, hit at, and wrestle. RT play was not associated with aggression, and the aggression factor had high loadings for different body movements including hit, push, and take-tug-grab. Unfortunately, body movements involved in play have not been a major focus of research among humans. While human ethologists (see Blurton Jones, 1972) initially focused on the movements performed by children when playing, most contemporary research on the play of children has focused less on the structural components of play and more on its social aspects.

IV. RT COMMUNICATION PATTERNS EXCLUSIVE TO PLAY

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

Rodents. In rodents, irrespective of the complexity of play, there is little evidence for the existence of specific play signals. There has been the suggestion of a play specific odor in one species of vole (*Micotus agrestis*) (Wilson, 1973) and during RT rats emit 50 kHz vocalizations (Knutson, Burgdorf, & Panksepp, 1998). However, play-specific odors have not been confirmed in other species, and the use of 50 kHz vocalizations is not restricted to play, but rather these calls are emitted in a variety of positively affective situations (Burgdorf, Kroes, Moskal, Pfaus, Brudzynski & Panksepp, 2008). It has yet to be determined whether these calls are performed specifically to solicit play or are simply a reflection of positive mood, although there is growing evidence suggesting that ultrasonic vocalizations (USVs) may also have communicative properties during emotionally charged behaviors (Brudzynski, 2013). For example, young rats will approach the source of 50 kHz calls when tested in a radial-arm maze and will also emit 50 kHz vocalizations during playback of these calls (Wohr & Schwarting, 2007). This suggests that young rats can be influenced by the playback of 50 kHz vocalizations in a manner that would be consistent with a communicative function but independent of playful engagement. Consistent with this possibility is the finding that young rats are more likely to emit vocalizations immediately before playful contact than when playful contact is terminated (Himmler, Kisko, Euston, Kolb & Pellis, 2014). Given the already vast literature directed towards understanding the neurobiological substrates of play in the rat (as recently reviewed in Siviy & Panksepp, 2011; Trezza, Baarendse, & Vanderschuren, 2010; Vanderschuren & Trezza, 2014), incorporating a sophisticated analysis of rat USVs with an ever-growing arsenal of improved neurobiological tools has great promise in better understanding how any putative communicative nature of ultrasonic vocalizations along with corresponding neural mechanisms.

More typically associated with play in rodents is the presence of locomotor-rotational movements (van Oortmersen, 1971; Pellis & Pellis, 1983), which appear to stimulate playful activity in the observer. Indeed, playfulness in one rat is contagious, making other animals engage in more play even if they have ceased playing due to fatigue or satiation (Pellis & McKenna, 1995; Reinhart, McIntyre, Metz, & Pellis, 2006; Trezza & Vanderschuren, 2008). An empirical question that arises from these findings is whether the playback of 50 kHz USVs can also stimulate playful activity in satiated rats.

Carnivores. The play bow is the most familiar carnivore-typical play signal. The performer bows in front of the playmate while wagging its tail and play panting (breathy exhalation) (Bekoff, 1995). Play bow is shown by most canids as well as by lions (Schaller, 1972) and, surprisingly, by Arabian babblers (*Turdoides squamiceps*) (Pozis-Francois, Zahavi, & Zahavi, 2004).

An anecdotal report on wolves illustrates the importance of the play bow as a signal to promote friendly contact (Stahler, Smith, & Landis, 2002). A 2.5 year old male from a neighboring pack attempted to join the all-female Yellowstone Druid pack. The Druid females used play bows both during their initial interactions with the unfamiliar male and also, apparently, as "acceptance" signals as their interactions became more intimate. These observations show that play signals can facilitate important life history transitions, such as immigration into a new group.

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

Fox (1970) described the early development of play faces in grey (*Urocyon cincreoargenteus*), red (*Vulpes vulpes*) and arctic (*Alopex lagopus*) foxes as well as in coyotes (*Canis latrans*) and wolves (*Canis lupus*). He emphasized "...that the facial expressions of the wolf and coyote are much more variable and show greater degrees of graduation...in contrast to the more stereotyped and less variable expressions of the foxes" (p. 59). Domestic dogs clearly illustrate this graduation in intensity of the canine play face. At low intensity, the mouth is relaxed, so that only the upper parts of the frontal lower teeth are visible. At a slightly higher intensity, the mouth is opened wider so that most or all of the bottom teeth can be seen. At highest intensity, the mouth is wide open so that both top and bottom teeth are visible (Handelman, 2008). The first two faces may be analogous to the primate play face and the third to the full play face of primates (see below).

Non-human primates. In some species of cercopithecines, head and torso rotations are body movements peculiar to play (Petrů, Špinka, Lhota, & Šípek, 2008), a pattern also present in many other mammalian lineages (e.g., Bekoff, 1974; Wilson & Kleiman, 1974; Byers, 1984; Donaldson, Newberry, Špinka, & Cloutier, 2002). In Hanuman langurs, a third of the play repertoire consists of patterns that are unique to play (Petrů et al., 2009). Some of these play-specific patterns may have a signaling function, as is probably the case of play face, eyes closing, or play gallop. Thus, they do not have a function beyond the boundary of play, but rather serve to keep the play going and thus allow other play elements to be performed and fulfill their function. Some other patterns (play tumble, head rotation, somersaults, flips, leaps) are also unique to play and may, therefore, serve as play signals. However, specialized signals are usually encoded in rather stereotypic movements to transmit information reliably (Morris, 1966; Zahavi, 1979; Hinde, 1982; McFarland, 1987) but Petrů *et al*. (2009) found these patterns very variable. Moreover, they were also present in solitary play, so how these actions function as possible play facilitating signals remains to be resolved.

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

In some cercopithecine species, the use and structure of particular facial expressions can converge as a function of their species-typical baseline levels of tolerance and affiliation (Thierry, Demaria, Preuschoft, & Desportes, 1989; Petit, Bertrand & Thierry, 2008). For example, in crested macaques (*Macaca nigra*), mandrills (*Mandrillus sphinx*) and geladas (*Theropithecus gelada*), the FPF is not a more intense version of PF but derives from the convergence between PF and the silent-bared teeth display, a facial expression used for affinitive purposes (van Hooff & Preuschoft, 2003; Bout & Thierry, 2005).

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

Whatever the origins and distribution of playful facial expressions may be, they have a pivotal role in managing playful interactions. The use of playful facial expressions is important to avoid any misunderstanding, cope with a playful interaction successfully, promote social affiliation, and favor cooperation (Pellis & Pellis, 2009). Adult geladas make an intense use of FPF that is a more effective and less ambiguous because it can be visually perceived at longer distances compared to PF (Palagi, 2008; Palagi & Mancini, 2011). FPF may also have an important role especially when play occurs in a social situation that is highly tense, such as that following intra-group aggression. Similarly, in humans, an increase in distress may be prevented by smiling appropriately, thus maintaining a cooperative mood during play (van Hooff, 1989). Play signals are not only the expression of an internal emotional state, but also, as has been shown in humans, they can have a manipulative function (Gervais & Wilson, 2005). There is evidence, for example, that great apes can use play signals in a strategic manner during play (Table 1). Adolescent chimpanzees increase their signal activity when the mothers of their younger playmates are witnessing the playful session, with facial expressions reaching peak levels of production when the roughness of their play is particularly high. Therefore, it appears evident that adolescent chimpanzees are able to fine-tune their playful facial displays not only to manage the session itself but also to manipulate the social context in which the session occurs in a sort of audience-effect (Flack, Jeannotte & de Waal, 2004).

In monkeys, the facial expressions are more fixed, whereas in hominoids they may show a gradient of intensity, which appears to be strictly associated with the positive emotions experienced by the subject (Parr, 2003). This phylogenetic distinction is supported by the observation that bonobos (like chimpanzees) sometimes exhibit a play face while engaging in solitary play (Palagi, 2008; Cordoni & Palagi, 2011; Palagi & Cordoni, 2012); this is not the case in macaques, capuchins, and marmosets (van Hooff & Preuschoft, 2003; de Marco & Visalberghi, 2007). Van Hooff and Preuschoft (2003, p. 257) affirmed that this ‘private emotional expression’ may suggest not only a playful intent directed to a potential partner but also a capacity for self-reflection or self-awareness, which are the precursors to more complex forms of cognition in social communication. However, the role of play signals in self-regulating emotional state may also occur in some monkey species (e.g., Pellis & Pellis, 2011; Pellis et al., 2011). For example, in spider monkeys (*Ateles geoffroyi*), head shaking facilitates amicable social contacts and occurs frequently during juvenile RT (Eisenberg & Kuehn, 1966). Yet, juvenile spider monkeys also shake their heads during solitary-locomotor play. Pellis and Pellis (2011) found that such headshakes occur in situations of uncertainty, such as when leaping from one branch to another, suggesting that headshaking is self-directed to promote action and take heart when confronting contexts of uncertainty. Similarly, a study of the use of the FPF in juvenile Tonkean macaques during social play found that about a third of their occurrences are best accounted for as being performed to regulate the performer's mood (Pellis et al., 2011).

Humans. Charles Darwin (1872) noted that human facial expressions have strong similarities with those of other animals. This similarity represents a shared heritage of our species, which supports the evolutionary continuity between humans and other mammals. According to some, the origin of human facial expressions, such as smiling, dates back to an ancestral nonhuman primate (de Waal, 2003; van Hooff & Preuschoft, 2003). Likewise, the play vocalizations of some non-human primates that are performed in conjunction with the play face are similar in many characteristics to the laughing associated with smiling during RT in humans (Vettin & Todt, 2005). Smiling and laughing are ubiquitous among humans and pervasive in play interactions. Socially elicited smiling occurs in early infancy (beginning near the end of the first month) and is one of the first signals of positive emotions (for review see Lewis 2000; Messinger, Mattson, Mahoor, & Cohn, 2012). Further, smiling among children and adults happens predominantly in social contexts where the signal can be observed (Bainum, Lounsbury, & Pollio, 1984; Provine & Fischer; 1989).

Researchers have long recognized that there are distinct forms and functions of smiling (e.g., Blurton-Jones, 1971; McGrew, 1972; Cheyne, 1976). Cheyne (1976) describes three main types of smiles observed among children: the upper smile, closed smile, and broad smile. The upper smile exposes the upper teeth while covering the lower teeth and is most common in friendly and affiliative interactions. All the teeth are covered in the closed smile and it is commonly observed in solitary play. The broad smile exposes both upper and lower teeth and characterizes social play, a form of smile that may be related to the FPF of chimpanzees (McGrew, 1972) and geladas (Palagi & Mancini, 2011). In an observational study of preschool children 2-4 year-olds, Cheyne (1976) found that the upper smile increased in frequency with age, whereas the other two types of smiles remained stable across each age. As social play becomes more prominent so does the upper smile, as the upper smile seems to signal and support social play.

Laughter is one of the first social vocalizations that human infants express, typically occurring between three and four months of age in response to social stimulation and tickling (Sroufe & Waters, 1976; Field, 1982). Human laughter is characterized by explosive and repetitive sound. Gervais and Wilson (2005) distinguish between two forms of human laughter: “Duchenne (stimulus-driven and emotionally valenced) and non-Duchenne (self-generated and emotionless) laughter” (p. 396) (Table 1). Gervais and Wilson (2005) stated that Duchenne laughter became ritualized in early hominids (4-2 mya) in order to favor playful emotional contagion. In the course of the biological and cultural evolution of humans, laughter has been gradually elaborated and co-opted to serve novel functions thus permitting the emergence of the "dark side" of human laughter, non-Duchenne laughter.

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

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

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

V. SELF-HANDICAPPING AND ROLE REVERSALS AS ASPECTS OF COMMUNICATION DURING RT

Self-handicapping, the ability of animals (including humans) to put themselves into unnecessarily disadvantageous or vulnerable positions or situations (Bekoff, 2001a,b; Bauer & Smuts, 2007), is a widespread phenomenon that occurs during play. Self-handicapping is typically considered to involve a reduction in the strength and velocity of movements when older animals play with younger ones. However, this underestimates the variety of different contexts and ways that different species can engage in self-handicapping. For example, a younger partner can engage in self-handicapping as well as its older partner (as occurs among dogs; Bauer & Smuts, 2007), and self-handicapping may also occur during solitary play when no partner is present (Petrů et al., 2008). Self-handicapping can arise as an animal orients its body in an unusual or unnatural position with respect to either its play partner or to the physical environment. Thus, self-handicapping can occur in three ways: social self-handicapping, such as when a stronger partner adopts an inferior posture, kinematic self-handicapping, such as when an animal adopts some physically demanding movements and postures, and sensory self-handicapping, such as when an animal closes its eyes when executing a movement (Petrů et al., 2009). Špinka et al. (2001) argued that self-handicapping movements involving awkward body positions are likely precursors for signals of an individual's playful intention. For example, as when one animal rolls over onto its back in front of partner as an invitation to play (Burghardt & Burghardt, 1972; LeResche, 1976). Even more striking is closing the eyes or covering the eyes while trying to catch a playmate (Kavanagh, 1978; Palagi, 2014; Russon & Vasey, 2012). These actions create self-handicapping situations that can be perceived by the playmate as a clear signal of benign intent (Table 1).

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

Rodents. While some rodent species exhibit high levels of solitary locomotor-rotational (SLR) play that stimulates others to engage in RT (Pellis & Pellis, 1983), others do not. For example, Syrian golden hamsters (*Mesocricetus auratus*) tend to be rather stolid creatures and, unlike rats, they never jump, run or pounce on one another (Pellis & Pellis, 1988). However, the complexity of the play is not correlated with the presence of SLR movements – hamsters have complex patterns of playful wrestling as do rats (Pellis & Pellis, 1987, 1988), and even though house mice have patterns of SLR play that are as exaggerated as those of rats (van Oortmerssen, 1971), their RT is limited to a simple pattern of approach-withdrawal (Pellis & Pasztor, 1999; Poole & Fish, 1975; Wolff, 1981). However, mice do show inter-animal coordination in some of their locomotor-rotational play (Terranova, Laviola, & Alleva, 1993; Laviola & Alleva, 1995), suggesting that even in a species with rudimentary social play, SLR movements may facilitate social engagement.

Carnivores. Among carnivores, self-handicapping and role reversals have only been systematically studied in domestic dogs. In a play group of 24 unrelated but familiar adult dogs, Bauer and Smuts (2007) found that in most playing pairs, one dog tended to adopt the offensive role significantly more often than the 50:50 rule would predict. The most dominant dog in the group hardly ever relinquished the offensive role during play, but many of the other dogs nevertheless sought her out for play, indicating that frequent role reversals are sometimes less important than other factors in determining play partner preferences. On the other hand, in a few dyads, roles were quite symmetric. This large variation across pairs may reflect differences in their relationship quality, with pairs that live together being more cooperative than those unfamiliar with one another. Also contrary to prediction, Bauer and Smuts (2007) found that younger dogs self-handicapped more than their older, more experienced partners did. Since younger dogs in general seem more eager to play than older dogs do, perhaps younger dogs self-handicapped more in order to induce older partners to play. This interpretation is consistent with the fact that younger animals also performed play signals more frequently than did their older partners (Bauer & Smuts, 2007). In a study of the development of play within litters, it was found that puppies developed specific play partner preferences which became more marked over time. Similar to adult dogs, young littermate pairs did not tend to follow the 50:50 rule, and their play became even more asymmetric with age (Ward, Bauer & Smuts, 2008; see also McNutt & Boggs, 1996 for similar findings in African wild dogs *Lycaon pictus*).

Nonhuman primates. Petrů et al. (2009) investigated the actions performed during play in five species of monkeys (*Semnopithecus entellus*, *Erythrocebus patas*, *Chlorocebus pygerythrus*, *Cercopithecus neglectus* and *Cercopithecus diana*). Of the 74 patterns characterized, 33 (45%) were judged to have a self-handicapping character. The self-handicapping patterns mostly involved making movements more physically demanding than necessary and exaggerating sensory input such as by performing somersaults and flips. Adult bonobos often engage in solitary energetic play sessions, where subjects challenge themselves in extremely acrobatic performances during which their vestibular apparatus is stimulated vigorously (Palagi & Paoli, 2007). At every age, bonobos love to climb, jump, dangle, and pirouette from supports in the environment while rapidly twisting. They often somersault on the ground covering several meters and alternate such performance with short and fast bouts of running (Palagi & Cordoni, 2012). Given that imitation can facilitate the social transmission of communicative signals (Miklósi, 1999), it is possible that the observation of another animal engaged in playful self-handicapping may increase the observer's motivation to play. Palagi (2008) tested the hypothesis of the social function of SLR play in adult bonobos. Bonobos use this communicatory tactic to elicit a playful response in the receiver: with about 50% of the solitary play sessions being followed by RT. Moreover, RT is more frequent when preceded by solitary play than by other self-directed behaviors, with pirouettes and somersaults being particularly frequent in the solitary play sessions directly preceding RT. However, care must be taken not to generalize from the findings of single species as the functions of such acrobatic movements and other postural maneuvers during RT may vary dramatically across species (Pellis, Pellis, Barrett & Henzi, 2014; Yanagi & Berman, 2014).

Humans. Children alternate between who is aggressing and who is the victim, with both partners self-handicapping (Pellegrini, 2009). For example, the “aggressor” may use exaggerated movements and open-handed hits and the “victim” may slow down to be caught or move into striking distance of the aggressor. In cases of adult-child play or in other unequal partnerships, the larger more competent and stronger partner typically self-handicaps (Pellegrini, 2009). Given that the amount of time spent in parent-offspring RT is positively correlated with children’s ability to translate bodily expressions into emotional states, it has been suggested that the ability to process play signals later with peers, may be rooted in the parent-offspring playful interactions (Parke, Cassidy, Burks, Carson & Boyum, 1992). Moreover, Pellegrini, Dupuis, and Smith (2007) posit that self-handicapping likely enhances the length of play bouts by increasing the players’ motivation and deterring boredom. Since RT gives opportunities to practice role reciprocation and self-handicapping, by playing with parents children can acquire an array of social strategies to engage in and maintain social interactions with peers (Pellegrini, 1993).

While relatively few studies have specifically focused on self-handicapping, restraint or role reversal in humans (Aldis, 1975; Smith & Boulton, 1990; Boulton, 1991), it seems likely that the use of self-handicapping during RT varies with age. For example, self-handicapping and restraining one’s strength appears to be less prominent in adolescence, an age at which RT provides a pathway to establish dominance relationships (Pellegrini, 2002). In infancy self-handicapping may promote proximity to peers which then may facilitate RT (Boulton, 1991), but data on such a linkage is wanting.

VI. LET’S SHARE OUR EMOTIONS! FACIAL AND BODY MIMICRY DURING PLAY

Matching one’s own behavior with that of others gives individuals the possibility to synchronize their activity with those of group members, to copy their behavior, and to place their behavioral activity in the appropriate context. The context of play, due to its plasticity, safety, and emotional involvement, provides a good substrate to investigate these mimicry processes. Experiencing others’ emotional states instantly allows an individual to foresee their playmates' intentions (Palagi, 2008) and fine-tune their motor sequences accordingly (Provine, 2000; Palagi & Mancini, 2011). So we can hypothesize that the ability to promptly respond with a mimicked action is an adaptive behavior.

Carnivores. Smuts (2007) argued that animals cooperating with one another in a "real" context (e.g., when resources or status are being contested) might negotiate their alliances first through synchronization of movements, which could occur during greetings, play or other contexts. Many different signals can be exchanged to negotiate cooperation, but they might not be honest. However, precise synchrony between different animals provides unmistakable evidence that two individuals are sufficiently invested in their relationship to be willing to expend time and effort to achieve such synchrony (Smuts, 2007). For example, in a bout of play in a pair of dogs, video analysis showed only 1/30th - 2/30th of a second occurred between the instant the first dog began to lower the forequarters and the second did so; in real time, the bows appeared perfectly synchronous (Smuts, 2007). While further study is needed, for present purposes we provisionally classify the play bow as an intentional, audience-dependent signal (*sensu* Horowitz, 2009) (Table 1).

Primates. In primates, different forms of imitation can be distinguished. Some forms are under voluntary and cognitive control, while others are involuntary, more linked to the emotions (Dimberg, Thunberg, & Elmehed, 2000; Iacoboni, 2009). For example, in humans, there are two possible responses to positive facial expressions: automatic responses (within 1.0 s), such as Duchenne smiles, and non-automatic responses (within 5.0 s), such as non-Duchenne smiles (Dimberg et al., 2000; Wild, Erb, Eyb, Bartels, & Grodd, 2003). The involuntary, automatic, mirroring and rapid response (e.g. the Duchenne smile, Table 1) given by the receiver is called Rapid Facial Mimicry (RFM) and can be distinguished from other forms of imitation (Iacoboni, 2009) by the rapidity of the matched reply. RFM plays an important role in emotional contagion by affecting one another's emotions or state of arousal (Davila-

Ross, Menzler, & Zimmermann, 2008; de Waal, 2008). There is evidence that facial mimicry in playful contexts correlates with the success of playful interactions. For example in chimpanzees, play bouts last more when the play face is bidirectionally performed by the two players (Waller & Dunbar, 2005). Moreover, social play sessions characterized by facial replication last longer than those sessions punctuated only by spontaneous laughter (Davila-Ross, Allcock, Thomas, & Bard, 2011). It seems, therefore, that the emotional synchronization through facial mimicry goes hand in hand with the cooperative side of social play. In humans, facial responsiveness requires a mechanism of "redirection of the sender's neural processing and perception toward one interactant and away from others" (Schmidt & Cohn, 2001, p. 14). For both sender and receiver, maintaining a social interaction and exchanging facial signals requires investment in focused attention to the partner, which, in turn, can lead to costs, such as lost opportunities to interact with others and scanning the environment for danger. Data on geladas supports this hypothesis, as the duration of play is positively correlated with RFM but not with delayed facial mimicry (Mancini et al., 2013a, Mancini, Ferrari, & Palagi, 2013b).

VII. MAKE A GESTURE TO TELL ME SOMETHING! GESTURES AS A COGNITIVE BREAKTHROUGH

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

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

In apes, gestures are narrowly defined as movements of hands, feet, or limbs with communicative function. One of the reasons to keep gestures apart from other forms of bodily communication (e.g., canine play bow) is that the two are neurologically distinct in both production and perception by others (Pollick & de Waal, 2007). A single brachio-manual gesture may communicate different messages depending on the social context in which the gesture is used (Tomasello & Call, 1997). This kind of dissociation between gesture and context has been observed in all great ape species, including humans (Bruner 1975; Call & Tomasello, 2007), and in all contexts, including play.

Different from other forms of communication more strictly linked to emotional components (i.e., vocalizations and facial expressions), gestures are mainly based on cognitive capacities and experience (Table 1). In the great apes, one of the proposed learning processes for improvement of the gestural repertoire is that of “ontogenetic ritualization”, which is the capacity to create or invent new communicative signals by modifying pre-existing behavioral patterns (Tomasello & Call, 1997), so that a non-communicative pattern becomes communicative. For example, juvenile chimpanzees may initiate a play bout by slapping a potential playmate. If the receiver realizes that a play interaction often begins with the initiator raising an arm in preparation for slapping, the former may anticipate by responding playfully before actually receiving a slap. By noticing the anticipation of the receiver, the initiator may realize that the arm raising by itself is sufficient to elicit a playful response and thus, use that arm movement to elicit play (Tomasello, 1990). Although most evidence of ontogenetic ritualization is reported for immature subjects, it also appears plausible that adult apes are able to understand the cause-effect of a gesture, anticipate its function and, consequently, use a modified version of that gesture as a communicative signal (Palagi, 2008). There has been controversy, in recent literature, about the ontogeny of the intentional gestures of great apes (Hobaiter and Byrne, 2011a,b). Although the hypothesis of ontogenetic ritualization was able to account for the data reported in several studies, more recently doubts about it have arisen. Particularly, Genty, Breuer, Hobaiter, and Byrne (2009) comparing several gorilla populations, found no clear support for the hypothesis and detected no evidence that subjects had acquired novel gestures by imitation or other means of social transfer from conspecifics, such as population-specific differences in repertoire. They proposed that gorillas' gestures are species-typical as a result of genetic channeling in development, as with communicative signals of most other animals.

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

In all ape species, a great variety of gestures has been reported both in the wild and in captivity (Hobaiter & Byrne, 2011a,b, 2014). The gestural repertoire initially increases with age reaching the climax between the age of three-six years, and decreases again in adulthood (Tomasello & Call, 1997;

Call & Tomasello, 2007; Hobaiter & Byrne, 2011a), thus following the same ontogenetic trajectory as RT (Fagen, 1993). Even though there remain unresolved issues, the findings on great apes show that gestures are extensively used during play.

Gestural communication during playful interactions seems to be shaped also by the social structure of the species, with the highest frequency reported in the two *Pan* species (about 55% for bonobos, Pika et al., 2005; 47-70% for captive chimpanzees, Tomasello & Call, 1997; 40-63.4% for wild chimpanzees, Hobaiter & Byrne, 2011b), species that share a fission-fusion social system, characterized by fluid social interactions (Palagi, 2006). A slightly lower percentage (about 40%) has been reported for gorillas, which live in a one-male society (Fleagle, 1999), where adult relationships are limited to spatial proximity rather than affinitive closeness. The lowest percentage of gestures in the playful context has been observed in orangutans (about 22%) that live a more solitary life-style (Fleagle, 1999; van Schaik, 1999). In the two *Pan* species, playful interactions can frequently involve adults, whereas in gorillas and orangutans playful activities are more limited to immature subjects (Palagi et al., 2007). Considering the importance of the gestural repertoire for the playful context, social play in all its forms may represent an opportunity to train the communicative plasticity that is necessary to acquire gestures and to use them in an appropriate manner. Such cognitive plasticity in the use of gestural communication deserves much more attention by scholars of play and intentional communication systems. Some authors (Genty et al., 2009; Hobaiter & Byrne, 2011a) did not find any evidence of ontogenetic ritualization or social learning, leading them to conclude that, “naturally communicative gestures of great apes may, in their ontogeny, be more similar to primate vocalizations than has been realized.” However, understanding the way apes and other primates communicate through gestures and how this capacity develops, becomes central when considering that it has been proposed that our ancestors’ first linguistic expressions were in the gestural domain, more than in the vocal domain (Corballis, 2002). This hypothesis also seems to be supported by some neurological findings suggesting that human language probably has developed from gestural communication (Cantalupo & Hopkins, 2001; Hopkins, Russell, & Cantalupo, 2007).

VIII. CONCLUSIONS AND FURTHER DIRECTIONS

1) Play behavior, especially social play in the form of RT, due to its plasticity and versatility, is a complex phenomenon that challenges not only players but also scholars. Play may thus offer an avenue to study the precursors from which some forms of animal communication have evolved. Animal communication is certainly phylogenetically much older than play behavior, but play has provided a rich background for the development of flexibility in animal communication (Fagen, 1981, 1993).

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

3) We categorized signals used during play along two dimensions, each offering new insights and opportunities for cross-species comparisons.

(i) In the first dimension, it is recognized that some signals are based on patterns recruited from other functional contexts (see the left side of Table 1), others are patterns exclusively designed for play (see the right side of Table 1) and both these kinds of signals can serve similar functions. This theoretical categorization permits the delineation of, from a functional point of view, a common platform of play communication across different *taxa* thus favoring a comparative approach.

(ii) The second dimension is related to the proximate mechanisms that produces the signals. Some signals are driven by the emotions, and so relatively involuntary (lower part of Table 1) while others by cognition, and so relatively intentional (upper part of Table 1). Some lineages of animals have exaggerated the inter-play between the emotional and intentional aspects of play signals, yielding admixtures of communication that have led to very complex forms of RT. For example, rodents utilize both locomotor-rotational movements (intentional) and 50 kHz calls (emotional), both of which may serve to communicate the playful intentions of the participants. This blending of signals makes it difficult to distinguish intentional from non-intentional signals as from the receiver's perspective any signal that indicates the playful mood of the performer may be equally informative (Demuru et al., 2014). For instance, spontaneous laughter, which is the expression of a positive emotional state, can be read and cognitively utilized by the receiver to help manage the play session. If the laughter occurs during solitary play, the receiver can cognitively interpret the spontaneous, emotion-driven facial expression as a signal indicating the sender's propensity to engage in social play. The same may apply to self-handicapping and role reversal. They can be considered both intentional signals used strategically by animals to enhance play motivation of conspecifics and a form of emotionally self-rewarding action that can be interpreted by conspecifics as a signal of the benign intent of others.

4) Review of the play communication literature suggests that a sort of dualism between the emotional and intentional nature of a signal can be detected by applying a "shifting approach", whereby the emotional component of a signal can be revealed by analyzing its performance when the subject is alone (e.g., during solitary play) (Pellis & Pellis, 2011). The movements involved and their timing can be compared when the signal is performed during solitary play and when engaged in RT so as to reveal the performer's awareness of the presence of an audience (cognitive component) (Palagi, 2008; Yanagi & Berman, 2014). When the cognitive component comes into play, the signal can be enriched by new

elements (exaggeration, amplification, long-lasting performance, repetition) that improve its detection by a potential receiver.

5) Future studies need to bring together two avenues of investigation. First, as seen from the comparative survey, few species have been studied with the intensity needed to characterize the range and type of play signals used in their repertoire, much less the contexts in which different signals may be used. Given that much of what we know is derived from carnivores, primates and rodents, and that these represent highly diverse Orders, it seems only reasonable to recommend that a broader range of species in these, and possibly other, mammalian be added to the comparative data set. The independent radiations of marsupial mammals and birds may be particularly useful to test hypotheses derived from the currently limited data on placental mammals. Also, as shown in this review, there is considerable variation across species and lineages of species as to how complex the play can be, and, in part, these variations are likely to depend on the tactics used to ensure that interactions maintain the minimum degree of reciprocity needed for them to remain playful. Aside from these empirical requirements, the emerging comparative data set needs to be integrated with novel theoretical approaches. A deeper understanding about the functions of reciprocity, synchronicity and incongruity in interactions could be provided by mathematical modeling (e.g., game theory, Fagen, 1981; Dugatkin & Bekoff, 2003), which, in turn, could alert researchers to look for variations in behavior that are currently not considered. A better understanding about the range and use of play signals and how these are used to navigate the demands of reciprocity during play could then be used as a basis for analyses involving the methods of comparative biology to determine the factors that have promoted the evolution of signals along the dimensions that we have delineated (Table 1). Social systems that involve highly nuanced social relationships and expanded cognitive capacity (likely reflected in expansion of frontal areas of the cortex) seem to be promising factors to explore in this regard.

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Table legend

Table 1 - The figure shows the categorization of communicative signals commonly used in Rough-and-Tumble play. The table is organized according to two theoretical dimensions: signal specificity (signals designed for play - right side - and signals recruited from other functional contexts - left side) and proximate causes of signals (emotionally driven signals - lower part - and cognitively driven signals - upper part).

INTENTIONAL SIGNALS

PATTERNS RECRUITED FROM CONTEXTS OTHER PLAY

PATTERNS EXCLUSIVE TO PLAY

FACIAL EXPRESSIONS

Non-human primates: lipsmacking (macaques, baboons, geladas), bared teeth (macaques).
Humans: Non-Duchenne smile

BEHAVIORAL PATTERNS RECRUITED FROM OTHER CONTEXTS AND USED IN ROLE REVERSAL and SELF-HANDICAPPING

Carnivores: Inhibited bites (dogs, bears, hyenas) and clawing (black bears)
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).

BEHAVIORAL PATTERNS RECRUITED FROM OTHER CONTEXTS USED TO SOLICITE 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

FACIAL EXPRESSIONS

Non-human primates: Full play face in adult geladas. Play faces in juvenile chimpanzees in presence of a particular audience (e.g. the mother of the younger playmate).

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.

BODY POSTURES AND MOVEMENTS EXCLUSIVE OF PLAYFUL CONTEXT

Canids: play bow
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

BODY POSTURES AND MOVEMENTS

Canids: Play rolling and squirming during solitary play

FACIAL EXPRESSIONS

Non-human primates: Playful facial displays performed in the middle of a 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 context (non-Duchenne smile, see the upper-left quadrant)

BODY POSTURES AND MOVEMENTS

Rodents and Primates: Locomotor-rotational movements during solitary play
Primates: Head rotation in langur solitary play

EMOTIONAL SIGNALS

Running head: *Social play and communication in animals*

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

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ABSTRACT

Rough-and-tumble play (RT) is a widespread phenomenon in mammals. Since it involves competition, whereby one animal attempts to gain advantage over another, RT runs the risk of escalation to serious fighting. Competition is typically curtailed by some degree of cooperation and different signals help negotiate potential mishaps during RT. This review provides a framework for such signals, showing that they range along two dimensions: one from signals borrowed from other functional contexts to ones that are unique to play, and the other from purely emotional expressions to highly cognitive (intentional) constructions. Some animal taxa have exaggerated the emotional and cognitive inter-play aspects of play signals, yielding admixtures of communication that have led to complex forms of RT. This complexity has been further exaggerated in some lineages by the development of specific novel gestures that can be used to negotiate playful mood and entice reluctant partners. Play-derived gestures may provide new mechanisms by which more sophisticated communication forms can evolve. Therefore, RT and playful communication provide a window into the study of social cognition, emotional regulation and the evolution of communicative systems.

Key words: Intentional signals; emotional signals; gestures; facial expressions; self-handicapping behavior

CONTENTS

I. INTRODUCTION

Defining play is a difficult matter. Compared to so-called “serious” behaviors, whose functions are more readily discerned, play remains an intriguing challenge. Burghardt (2005, 2011) developed five criteria with which to identify play. (1) Play is not completely functional in the form or context in which it is performed because it does not seem to contribute to current survival. (2) Play is spontaneous, voluntary, intentional, pleasurable, rewarding, reinforcing, or autotelic (“done for its own sake”). (3) Compared to other ethotypic behaviors, play is incomplete, exaggerated, awkward, or precocious and it generally involves patterns modified in their form, sequencing, or targeting. (4) During a play session, the behavioral pattern is performed repeatedly but not in a manner that is rigidly stereotyped. (5) Play is initiated when animals are relatively free from environmental and social stressors.

Beyond its definition, among all social activities, social play stands out for its versatility, plasticity, and unpredictability (Fagen, 1993; Špinka, Newberry, & Bekoff, 2001; Burghardt, 2005, 2012; Palagi, Antonacci, & Cordoni, 2007). Nonetheless, social play does follow rules that, if violated, can lead to serious aggression (Pellis & Pellis, 1998a; Pellis, Pellis, & Reinhart, 2010). While rules are followed in both free play (e.g., play fighting) and structured games (e.g., rugby matches), the nature of the rules differs (Power, 2000; Burghardt, 2005). Structured games, unlike free play, are built on *a priori* rules and the participants have to follow these rules to avoid being penalized. In "free play" the rules to be followed are created by the players. Depending on the players involved (gender, rank, age, size, kin) and the kind of play performed (tickling, locomotor-rotational activities, fighting), each new play session requires the application of ‘flexible rules’ that can be continually redefined (Pellegrini, 2009). Also, unlike structured games where the rules may be enforced by a third party (e.g., umpire), during free play enforcement of the rules is by the players themselves. These rules could be grounded in affective (e.g., emotional synchrony) or cognitive domains (e.g., intentionality), or some combination of both (Demuru, Ferrari, & Palagi, 2014). Therefore, managing new playful interactions requires sophisticated communicative skills. Social play can also involve considerable communicative effort, improvisation, strategic timing, and creativity. Thus, play may be more mentally demanding than most other non-aggressive behaviors. Indeed, comparative studies of primates have shown that those species that engage in more social play, but not in non-social play, have an enlargement of several brain areas involved in regulating play (Graham & Burghardt, 2010). Because of these demands on flexibility and improvisation during social play, this behavior has been hypothesized to be the engine of much behavioral innovation (Fagen, 1993). We suggest that it is also the reason why social play is an ideal context to study communication and cognition.

II. WHY COMMUNICATION IS FUNDAMENTAL FOR ROUGH-AND-TUMBLE (RT) PLAY

Social play, especially rough-and-tumble play (RT), is intimately associated with communication. Play communication may be among the most complex communication system seen in humans and non-humans. In its most elemental form, communication can be characterized as a behavior that is performed for the advantage of the signaler (Burghardt, 1970). The prolonged reciprocal interactions that occur during play involve a situation in which the players are, often simultaneously, both signalers and receivers.

Despite its seemingly free-flowing appearance, RT can be quite a complex form of social play, because it involves physical contact between partners and may include patterns typical of real fighting. Although there are rules of interaction that distinguish RT from its serious counterparts (Pellis *et al.*, 2010), ambiguous situations arise, such as a playful attack that occurs unexpectedly. In such cases, additional information, such as that provided by particular signals, are important (Aldis, 1975). Although not invariably unambiguous themselves (Pellis & Pellis, 1996, 1997), in many circumstances, these signals can reduce the uncertainty arising from contact during play (Palagi, 2008, 2009). Specific actions, gestures, gaits, vocalizations, facial expressions, and even odors may communicate the playfulness of a potentially dangerous act (Fagen, 1981; Bekoff, 2001a; Palagi, 2006). Signals can help to avoid escalation to real aggression and may prolong play (Burghardt, 2005; Waller & Dunbar, 2005; Mancini, Ferrari, & Palagi, 2013a). Bekoff (1995) stressed the importance of play signals as "punctuation" during playful interactions, especially when play includes elements of hostility**.** Moreover, communicative signals can also have a major role in expressing positive emotions, making the session pleasurable and rewarding for the players (Kuczaj & Horback, 2013). Managing a playful interaction successfully can favor the development of cooperation beyond the play session itself (Palagi & Cordoni, 2012).

RT uses movements, postures and signals recruited from other functional behaviors (e.g., predatory, antipredatory, mating, intra-species agonism) (Bekoff & Byers, 1981; Fagen, 1981, 1993; Pellis, 1988). Some of the gestures used in RT are unique to play (Petrů, Špinka, Charvátová, & Lhota, 2009). Distinguishing between those gestures that are unique and those that are derived from other contexts is often not easy to make for a specific behavioral pattern as making this distinction depends on the thoroughness of the knowledge on the behavioral repertoire of the species being considered. For some species, the repertoire is known sufficiently well to sometimes be able to make this distinction. Chasing-pouncing and lip-smacking are examples of patterns recruited from other functional contexts such as aggression and grooming, respectively. Play bows (Bekoff, 1995), head rotation (Petrů *et al.*, 2009), tickling (van Lawick-Goodall, 1968), vocalizations (Rasa, 1984) and some versions of play faces (Pellis & Pellis, 1997; Palagi, 2008) are patterns that seem to be unique to play (Table 1).

Communication during RT can also vary along another dimension. At one extreme are behaviors such as those facial expressions that are not influenced by the audience and so appear to be primarily determined by the emotional state of the performer (emotional signals) (Cordoni & Palagi, 2011; Pellis, Pellis, Reinhart, & Thierry, 2011). At the other extreme are audience-dependent signals directly targeted to a particular recipient or specific audience (intentional signals), which appear to be produced so as to influence their potential partners' playful behavior (Hobaiter & Byrne, 2011a). Some authors argue that intentionality and emotionality are not mutually exclusive in the signal production process but, rather, may represent two mechanisms that interact during signal production (Liebal, Waller, Burrows & Slocombe, 2014; Demuru et al., 2014). Indeed, some of the signals used during RT fall in between these extremes (Table 1).

This framework is useful because it includes many different kinds of signals that communicate play. Some of these signals, such as the relaxed open mouth, have ancient evolutionary roots and are, therefore, shared among many species. Others, such as play solicitation signals, are highly variable across species, so that particular variants are limited to specific lineages that take highly variable forms across different species.

Although RT has been described in many eutherian and marsupial mammals as well as in some other vertebrates, including birds and frogs (Burghardt, 2005), here we focus on the extensive research available on the most commonly studied mammalian taxa: rodents, carnivores, non-human primates, and humans.

III. RT COMMUNICATION PATTERNS RECRUITED FROM OTHER FUNCTIONAL BEHAVIORS

The incorporation and elaboration of communication signals across functional behavior systems, termed ritualization, is well known in the contexts of feeding, courtship, agonism and parent-offspring interactions (Cullen, 1966; Thorpe, 1966; Burghardt, 1973; Foster, 1995). That play not only recruits ritualized behavior, but may also be the source for new ritualized behavior has not been sufficiently recognized (Burghardt, 2012).

During serious fighting, animals use tactics of attack to deliver blows or bites and tactics of defense to block those strikes. Attacking animals face the threat of retaliation, as a successful parry can be followed by a counterattack by the original defender (Geist, 1978). To attack effectively while minimizing the likelihood of retaliation, offensive maneuvers frequently incorporate a defensive component (Pellis, 1997). The situation is different in RT, that to remain playful it has to be reciprocal (Altmann, 1962; Dugatkin & Bekoff, 2003). During RT animals' maneuvers often work to facilitate role reversals (i.e., successful counterattacks), by either not incorporating defensive actions during attacks (Pellis & Pellis, 1998a), or by not capitalizing on the advantage that has been gained (Pellis *et al*., 2010).

Rodents. RT has been reported in a wide range of rodents (for reviews see Fagen, 1981; Pellis & Pellis, 2009), an order that encompasses some 40% of all mammals (Nowak, 1999). A survey of RT in this order highlights several important lessons that need to be investigated in greater depth across more lineages of mammals (Pellis & Iwaniuk, 2004). First, it shows that the targets being competed over can be derived from functional contexts associated with aggression, predation, sex and other forms of amicable contact (e.g., greeting, grooming). Moreover, there are identifiable phylogenetic trends; the RT of most species of murid rodents thus far studied involves sexual targets, whereas in the other major branches of the order, the sciurids and hystricognaths, there are sub-lineages that compete solely over sexual targets or aggressive targets, and some do both. Second, not all members of this order engage in play fighting (e.g., Happold, 1976), and for those that do, there are gradations of complexity. This can range from playfully pouncing on and contacting the play target, but without the recipient responding (Wilson, 1973), to attacking the target with vigorous defense that involves extensive wrestling (Goldman & Swanson, 1975). In between, there is attack with the defense limited to fleeing (Wolff, 1981). Even among species that have complex wrestling, there can be considerable variation in the frequency with which the most complex form of wrestling play occurs (Pellis, Pellis & Dewsbury, 1989). Third, irrespective of the source of the target competed over during RT, the animals engage in play in manner that increases the likelihood of role reversals (Pellis, Pellis & Foroud, 2005; Pellis et al., 2010), so increasing the likelihood that RT remain playful and does not escalate into aggression (Bekoff, 2001a, b). The extensive experimental work on rats, in particular, has also begun to reveal how multiple levels of neural control mechanisms may been added over evolutionary time in some lineages (Pellis & Iwaniuk, 2004; Pellis & Pellis, 2009). These insights into the neurobiology of RT may also provide a framework for understanding how more cognitively sophisticated signaling systems used in the play of some animals (Table 1) may have evolved.

Most of what has been learned about the neurobiology of RT (Cheng, Taravosh-Lahn & Delville, 2008; Siviy & Panksepp, 2011; Vanderschuren, Niesink & Van Ree, 1997) and the roles that RT has in shaping the development of the brain and social skills (Pellis & Pellis, 2009; Vanderschuren & Trezza, 2014; Wommack, Taravosh-Lahn, David & Delville, 2003), has come from the study of two species, the rat (*Rattus norvegicus*) and the Syrian golden hamster (*Mesocricetus auratus*). With regard to play signals, there has been less intensive work on these species, but there are some such potential signals in rats, that could open the way to test some of the hypotheses generated here.

During RT, rats attack and defend the nape of the neck, which if contacted is nuzzled with the snout (Pellis & Pellis, 1987; Siviy & Panksepp, 1987), whereas during serious fighting, biting attacks are directed at the rump and lower flanks and the face (Blanchard & Blanchard, 1977). Nape attack during RT in rats is blocked by the use of a variety of defensive tactics, with the most common in the juvenile period being to roll over to supine, which leads to the attacker standing over the supine partner (i.e., pin configuration). From this position, they continue to compete for access to their partner's nape

(Panksepp, 1981; Pellis & Pellis, 1987). Rats that have been decorticated at birth grow into juveniles and young adults that are able to engage their peers in RT (Panksepp, Normansell, Cox & Siviy, 1994; Pellis, Pellis & Whishaw, 1992). Most critically, RT of the decorticate rats has the same reciprocal character as RT involving intact rats, suggesting that the ability to follow the rules that keep RT playful involves mechanisms that reside deeper in the brain (Pellis et al., 2010). That is, higher-level cognitive functions that require the cortex (Kolb & Whishaw, 2009) are not needed for complex RT.

The experience of RT in the juvenile period enhances the development of executive functions that includes impulse control (Baarendse, Counotte, O'Donnell & Vanderschuren, 2013) - the ability to 'think before you act' that may be necessary in rough play. The way that juvenile RT experience may do so is by modifying the prefrontal cortex, the area of the cortex associated with executive functions (Vanderschuren & Trezza, 2014). As already noted, RT between pairs of juvenile rats can proceed in a seemingly normal manner in the absence of the entire cortex. However, RT becomes more complex as rats become young adults, when males use a rougher version of RT as a tool for negotiating dominance relationships (Pellis, Hastings, Shimizu, Kamitakahara, Komorowska, Forgie & Kolb, 2005). Adult rats are able to modify the roughness of their play depending on the identity of their partner and on the partner's movements: an ability that is abolished by lesions of the prefrontal cortex (Bell, McCaffrey, Forgie, Kolb & Pellis, 2009; Pellis et al., 2006). This suggests that the cortex, especially the prefrontal cortex, may be critically important when RT occurs in more ambiguous situations (e.g., between partners that differ in size or status, when multiple partners are involved). That is, while the basic skills needed to engage in RT do not require sophisticated cognitive functions, RT can occur in situations in which more sophisticated processing needs to be deployed.

In rodents, the role of postural and movement-related facilitators of play is probably greater than in lineages with a richer repertoire of specific play signals (such as the carnivores and primates discussed below). Thus, in rats, the fighting movements performed during play incorporate self-handicapping postures (Table 1). Nonetheless, experimental findings in rats with damage to the prefrontal cortex show that, in some situations, these play facilitating maneuvers may require the involvement of more sophisticated cognitive processing. Given that the prefrontal cortex is involved in a range of executive functions, with particular sub-regions dealing with particular aspects of decision making (Euston, Gruber & McNaughton, 2012), and that, in some situations, RT can proceed relatively normally in the absence of such cortical mechanisms (Panksepp et al., 1994; Pellis et al., 1992), it suggests that such executive functions preceded the evolution of play, the core circuitry for which involves subcortical mechanisms (Panksepp, 1998; Siviy & Panksepp, 2011; Vanderschuren et al., 1997). For some lineages, where RT has become more complex or has been usurped for novel functions, such as negotiating social relationships (Palagi, 2006; Pellis, 2002), the prefrontal mechanisms may have been co-opted for a more critical involvement in RT.

Unfortunately, as noted above, there are few candidate signals for use in RT by rodents, and those that have been identified have yet to be fully investigated. Conversely, as shown in the proceeding sections, many more, and better studied, examples of play signals are available from other mammalian orders, but much less experimental work on the mechanisms involved is available in these non-rodent species. Therefore, while experimental studies on rats can provide clues as to how play signaling may have evolved increasingly sophisticated neural control, descriptive studies afforded by dogs, monkeys and apes, provide an appreciation for the potential range and complexity of play signals. Such an appreciation can then lead to research questions that may be experimentally tested with rats. As will be explored further below, vocalizations emitted during the RT of rats (Panksepp & Burgdorff, 2003) may provide the kinds of signals that span the range of complexity of play signals suggested in this paper (Table 1).

Carnivores. Domestic dog RT involves several different types of movements (Bauer & Smuts, 2007; Handelman, 2008), which are not strict categories, since elements from any one type may be included in or interspersed with other types. RT among adult wolves has not been systematically described, but it appears to involve all of the play behaviors shown by dogs and, probably, a few others (Cordoni, 2009). In wolves, the first four-six weeks of life are characterized by high frequencies of games involving mimicking, during which the two cubs imitate each other's facial expressions (muzzle-wrinkling, lip-retraction) without being in physical contact (Feddersen-Petersen, 1991). In contrast to wolves, for poodles, games in which they mimic one another mainly involve playful communication in the acoustic modality (e.g. bark games). This form of acoustic play reaches its peak during the fourth month of life (Feddersen-Petersen, 1991).

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

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

Nonhuman primates. Given that primates vary greatly in social systems, rate of development and other socioecological factors (Nowak, 1999), this taxon provides the opportunity to gain a comprehensive understanding of the roles of play communication and the cognitive skills required supporting such communication (Armstrong, 1985). For example, lemurs are relatively small brained, form an independent primate radiation and are more similar to ancestral group-living primates than the more intensively studied monkeys and apes (Tattersall, 1982). The ringtail lemur (*Lemur catta*) is a diurnal and highly terrestrial species, which forms multimale/multifemale social groups characterized by female dominance and male dispersal. The white and black tail of this species is used to communicate and regulate many aspects of social life. The "stink fights" engaged in by males during their agonistic interactions are the most striking example (Jolly, 1966). Males place their tails between the legs and upward in front of the torso and anoint them with the secretion produced by specialized antebrachial glands on wrist and forearm (*anoint-tail).* Then, the animal may repeatedly flick the tail downward over the top of its head to spread the odor secretion (*wave-tail*). During the agonistic wave-tail pattern, with his ears flattened against the top of his head, the male faces and gazes at the opponent. Mature males also anoint and wave their tails toward females as signals of appeasement or even submission during courtship (solicitation of copulation; Jolly, 1966). There is also a playful version of the communication pattern involving tail use (Jolly, 1966): a good example of a pattern recruited from other functional contexts to communicate during play.

During RT, ringtailed lemurs anoint their tails neither facing the playmate nor even gazing at the playmate (tail-play). Infants begin to perform tail-play during the weaning period (6 months; Palagi, Gregorace, & Borgognini Tarli, 2002). Analysis of the dynamics of RT in juvenile ringtail lemurs indicates that such play resembles real aggression (Pellis & Pellis, 1997). In a number of species, adult RT has been reported to be rougher, having a greater likelihood of escalation into serious fighting (Fagen, 1981; Pellis, 2002; Palagi & Cordoni, 2012). However, the low levels of escalation found in lemurs (Palagi, 2009) suggest that they are able to cope with possible ambiguous situations, with tail-play probably having a role. During play, males generally direct tail-play mostly toward females, which can be very aggressive toward them (Jolly, 1966). Hence, playing with females may be particularly risky for males, who need to clearly signal their own "playful intentions" to avoid misinterpretation. Ringtailed lemurs also frequently use tail-play when playing with less-familiar group members (as determined by low grooming rates). When play occurs between potentially dangerous partners, RT is often characterized by a redundancy of signals (Bekoff, 1974; Henry & Herrero, 1974; Power, 2000). In fact, RT between two individuals, which socially interact at a very low frequency, may be particularly unsafe due to the limited information (physical strength, self-handicapping skill, and movement rapidity) they have about each other.

Humans. In humans, structural descriptions of play have focused on three main characteristics: exaggeration, sequence variability and incompleteness (Pellegrini, 2009). Specific body movements alone, like running and jumping, are not necessarily indicative of play. Instead, play movements are recognized when associated with a constellation of features; for example, exhibiting a play face while jumping on one leg, balancing, swinging, sliding, running in an exaggerated manner or running with a variable sequence (e.g., zig-zagging). Incomplete body movements, like punching near a play partner's arm but not actually making contact, are also used as communication during play. Blurton Jones (1972), in an observational study of 2- and 4-year-olds, found in a factor analysis that the RT play factor had high loadings for laughing-play face, run, jump, hit at, and wrestle. RT play was not associated with aggression, and the aggression factor had high loadings for different body movements including hit, push, and take-tug-grab. Unfortunately, body movements involved in play have not been a major focus of research among humans. While human ethologists (see Blurton Jones, 1972) initially focused on the movements performed by children when playing, most contemporary research on the play of children has focused less on the structural components of play and more on its social aspects.

IV. RT COMMUNICATION PATTERNS EXCLUSIVE TO PLAY

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

Rodents. In rodents, irrespective of the complexity of play, there is little evidence for the existence of specific play signals. There has been the suggestion of a play specific odor in one species of vole (*Micotus agrestis*) (Wilson, 1973) and during RT rats emit 50 kHz vocalizations (Knutson, Burgdorf, & Panksepp, 1998). However, play-specific odors have not been confirmed in other species, and the use of 50 kHz vocalizations is not restricted to play, but rather these calls are emitted in a variety of positively affective situations (Burgdorf, Kroes, Moskal, Pfaus, Brudzynski & Panksepp, 2008). It has yet to be determined whether these calls are performed specifically to solicit play or are simply a reflection of positive mood, although there is growing evidence suggesting that ultrasonic vocalizations (USVs) may also have communicative properties during emotionally charged behaviors (Brudzynski, 2013). For example, young rats will approach the source of 50 kHz calls when tested in a radial-arm maze and will also emit 50 kHz vocalizations during playback of these calls (Wohr & Schwarting, 2007). This suggests that young rats can be influenced by the playback of 50 kHz vocalizations in a manner that would be consistent with a communicative function but independent of playful engagement. Consistent with this possibility is the finding that young rats are more likely to emit vocalizations immediately before playful contact than when playful contact is terminated (Himmler, Kisko, Euston, Kolb & Pellis, 2014). Given the already vast literature directed towards understanding the neurobiological substrates of play in the rat (as recently reviewed in Siviy & Panksepp, 2011; Trezza, Baarendse, & Vanderschuren, 2010; Vanderschuren & Trezza, 2014), incorporating a sophisticated analysis of rat USVs with an ever-growing arsenal of improved neurobiological tools has great promise in better understanding how any putative communicative nature of ultrasonic vocalizations along with corresponding neural mechanisms.

More typically associated with play in rodents is the presence of locomotor-rotational movements (van Oortmersen, 1971; Pellis & Pellis, 1983), which appear to stimulate playful activity in the observer. Indeed, playfulness in one rat is contagious, making other animals engage in more play even if they have ceased playing due to fatigue or satiation (Pellis & McKenna, 1995; Reinhart, McIntyre, Metz, & Pellis, 2006; Trezza & Vanderschuren, 2008). An empirical question that arises from these findings is whether the playback of 50 kHz USVs can also stimulate playful activity in satiated rats.

Carnivores. The play bow is the most familiar carnivore-typical play signal. The performer bows in front of the playmate while wagging its tail and play panting (breathy exhalation) (Bekoff, 1995). Play bow is shown by most canids as well as by lions (Schaller, 1972) and, surprisingly, by Arabian babblers (*Turdoides squamiceps*) (Pozis-Francois, Zahavi, & Zahavi, 2004).

An anecdotal report on wolves illustrates the importance of the play bow as a signal to promote friendly contact (Stahler, Smith, & Landis, 2002). A 2.5 year old male from a neighboring pack attempted to join the all-female Yellowstone Druid pack. The Druid females used play bows both during their initial interactions with the unfamiliar male and also, apparently, as "acceptance" signals as their interactions became more intimate. These observations show that play signals can facilitate important life history transitions, such as immigration into a new group.

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

Fox (1970) described the early development of play faces in grey (*Urocyon cincreoargenteus*), red (*Vulpes vulpes*) and arctic (*Alopex lagopus*) foxes as well as in coyotes (*Canis latrans*) and wolves (*Canis lupus*). He emphasized "...that the facial expressions of the wolf and coyote are much more variable and show greater degrees of graduation...in contrast to the more stereotyped and less variable expressions of the foxes" (p. 59). Domestic dogs clearly illustrate this graduation in intensity of the canine play face. At low intensity, the mouth is relaxed, so that only the upper parts of the frontal lower teeth are visible. At a slightly higher intensity, the mouth is opened wider so that most or all of the bottom teeth can be seen. At highest intensity, the mouth is wide open so that both top and bottom teeth are visible (Handelman, 2008). The first two faces may be analogous to the primate play face and the third to the full play face of primates (see below).

Non-human primates. In some species of cercopithecines, head and torso rotations are body movements peculiar to play (Petrů, Špinka, Lhota, & Šípek, 2008), a pattern also present in many other mammalian lineages (e.g., Bekoff, 1974; Wilson & Kleiman, 1974; Byers, 1984; Donaldson, Newberry, Špinka, & Cloutier, 2002). In Hanuman langurs, a third of the play repertoire consists of patterns that are unique to play (Petrů et al., 2009). Some of these play-specific patterns may have a signaling function, as is probably the case of play face, eyes closing, or play gallop. Thus, they do not have a function beyond the boundary of play, but rather serve to keep the play going and thus allow other play elements to be performed and fulfill their function. Some other patterns (play tumble, head rotation, somersaults, flips, leaps) are also unique to play and may, therefore, serve as play signals. However, specialized signals are usually encoded in rather stereotypic movements to transmit information reliably (Morris, 1966; Zahavi, 1979; Hinde, 1982; McFarland, 1987) but Petrů *et al*. (2009) found these patterns very variable. Moreover, they were also present in solitary play, so how these actions function as possible play facilitating signals remains to be resolved.

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

In some cercopithecine species, the use and structure of particular facial expressions can converge as a function of their species-typical baseline levels of tolerance and affiliation (Thierry, Demaria, Preuschoft, & Desportes, 1989; Petit, Bertrand & Thierry, 2008). For example, in crested macaques (*Macaca nigra*), mandrills (*Mandrillus sphinx*) and geladas (*Theropithecus gelada*), the FPF is not a more intense version of PF but derives from the convergence between PF and the silent-bared teeth display, a facial expression used for affinitive purposes (van Hooff & Preuschoft, 2003; Bout & Thierry, 2005).

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

Whatever the origins and distribution of playful facial expressions may be, they have a pivotal role in managing playful interactions. The use of playful facial expressions is important to avoid any misunderstanding, cope with a playful interaction successfully, promote social affiliation, and favor cooperation (Pellis & Pellis, 2009). Adult geladas make an intense use of FPF that is a more effective and less ambiguous because it can be visually perceived at longer distances compared to PF (Palagi, 2008; Palagi & Mancini, 2011). FPF may also have an important role especially when play occurs in a social situation that is highly tense, such as that following intra-group aggression. Similarly, in humans, an increase in distress may be prevented by smiling appropriately, thus maintaining a cooperative mood during play (van Hooff, 1989). Play signals are not only the expression of an internal emotional state, but also, as has been shown in humans, they can have a manipulative function (Gervais & Wilson, 2005). There is evidence, for example, that great apes can use play signals in a strategic manner during play (Table 1). Adolescent chimpanzees increase their signal activity when the mothers of their younger playmates are witnessing the playful session, with facial expressions reaching peak levels of production when the roughness of their play is particularly high. Therefore, it appears evident that adolescent chimpanzees are able to fine-tune their playful facial displays not only to manage the session itself but also to manipulate the social context in which the session occurs in a sort of audience-effect (Flack, Jeannotte & de Waal, 2004).

In monkeys, the facial expressions are more fixed, whereas in hominoids they may show a gradient of intensity, which appears to be strictly associated with the positive emotions experienced by the subject (Parr, 2003). This phylogenetic distinction is supported by the observation that bonobos (like chimpanzees) sometimes exhibit a play face while engaging in solitary play (Palagi, 2008; Cordoni & Palagi, 2011; Palagi & Cordoni, 2012); this is not the case in macaques, capuchins, and marmosets (van Hooff & Preuschoft, 2003; de Marco & Visalberghi, 2007). Van Hooff and Preuschoft (2003, p. 257) affirmed that this 'private emotional expression' may suggest not only a playful intent directed to a potential partner but also a capacity for self-reflection or self-awareness, which are the precursors to more complex forms of cognition in social communication. However, the role of play signals in self-regulating emotional state may also occur in some monkey species (e.g., Pellis & Pellis, 2011; Pellis et al., 2011). For example, in spider monkeys (*Ateles geoffroyi*), head shaking facilitates amicable social contacts and occurs frequently during juvenile RT (Eisenberg & Kuehn, 1966). Yet, juvenile spider monkeys also shake their heads during solitary-locomotor play. Pellis and Pellis (2011) found that such headshakes occur in situations of uncertainty, such as when leaping from one branch to another, suggesting that headshaking is self-directed to promote action and take heart when confronting contexts of uncertainty. Similarly, a study of the use of the FPF in juvenile Tonkean macaques during social play found that about a third of their occurrences are best accounted for as being performed to regulate the performer's mood (Pellis et al., 2011).

Humans. Charles Darwin (1872) noted that human facial expressions have strong similarities with those of other animals. This similarity represents a shared heritage of our species, which supports the evolutionary continuity between humans and other mammals. According to some, the origin of human facial expressions, such as smiling, dates back to an ancestral nonhuman primate (de Waal, 2003; van Hooff & Preuschoft, 2003). Likewise, the play vocalizations of some non-human primates that are performed in conjunction with the play face are similar in many characteristics to the laughing associated with smiling during RT in humans (Vettin & Todt, 2005). Smiling and laughing are ubiquitous among humans and pervasive in play interactions. Socially elicited smiling occurs in early infancy (beginning near the end of the first month) and is one of the first signals of positive emotions (for review see Lewis 2000; Messinger, Mattson, Mahoor, & Cohn, 2012). Further, smiling among children and adults happens predominantly in social contexts where the signal can be observed (Bainum, Lounsbury, & Pollio, 1984; Provine & Fischer; 1989).

Researchers have long recognized that there are distinct forms and functions of smiling (e.g., Blurton-Jones, 1971; McGrew, 1972; Cheyne, 1976). Cheyne (1976) describes three main types of smiles observed among children: the upper smile, closed smile, and broad smile. The upper smile exposes the upper teeth while covering the lower teeth and is most common in friendly and affiliative interactions. All the teeth are covered in the closed smile and it is commonly observed in solitary play. The broad smile exposes both upper and lower teeth and characterizes social play, a form of smile that may be related to the FPF of chimpanzees (McGrew, 1972) and geladas (Palagi & Mancini, 2011). In an observational study of preschool children 2-4 year-olds, Cheyne (1976) found that the upper smile increased in frequency with age, whereas the other two types of smiles remained stable across each age. As social play becomes more prominent so does the upper smile, as the upper smile seems to signal and support social play.

Laughter is one of the first social vocalizations that human infants express, typically occurring between three and four months of age in response to social stimulation and tickling (Sroufe & Waters, 1976; Field, 1982). Human laughter is characterized by explosive and repetitive sound. Gervais and Wilson (2005) distinguish between two forms of human laughter: "Duchenne (stimulus-driven and emotionally valenced) and non-Duchenne (self-generated and emotionless) laughter" (p. 396) (Table 1). Gervais and Wilson (2005) stated that Duchenne laughter became ritualized in early hominids (4-2 mya) in order to favor playful emotional contagion. In the course of the biological and cultural evolution of humans, laughter has been gradually elaborated and co-opted to serve novel functions thus permitting the emergence of the "dark side" of human laughter, non-Duchenne laughter.

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

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

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

V. SELF-HANDICAPPING AND ROLE REVERSALS AS ASPECTS OF COMMUNICATION DURING RT

Self-handicapping, the ability of animals (including humans) to put themselves into unnecessarily disadvantageous or vulnerable positions or situations (Bekoff, 2001a,b; Bauer & Smuts, 2007), is a widespread phenomenon that occurs during play. Self-handicapping is typically considered to involve a reduction in the strength and velocity of movements when older animals play with younger ones. However, this underestimates the variety of different contexts and ways that different species can engage in self-handicapping. For example, a younger partner can engage in self-handicapping as well as its older partner (as occurs among dogs; Bauer & Smuts, 2007), and self-handicapping may also occur during solitary play when no partner is present (Petrů et al., 2008). Self-handicapping can arise as an animal orients its body in an unusual or unnatural position with respect to either its play partner or to the physical environment. Thus, self-handicapping can occur in three ways: social self-handicapping, such as when a stronger partner adopts an inferior posture, kinematic self-handicapping, such as when an animal adopts some physically demanding movements and postures, and sensory self-handicapping, such as when an animal closes its eyes when executing a movement (Petrů et al., 2009). Špinka et al. (2001) argued that self-handicapping movements involving awkward body positions are likely precursors for signals of an individual's playful intention. For example, as when one animal rolls over onto its back in front of partner as an invitation to play (Burghardt & Burghardt, 1972; LeResche, 1976). Even more striking is closing the eyes or covering the eyes while trying to catch a playmate (Kavanagh, 1978; Palagi, 2014; Russon & Vasey, 2012). These actions create self-handicapping situations that can be perceived by the playmate as a clear signal of benign intent (Table 1).

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

Rodents. While some rodent species exhibit high levels of solitary locomotor-rotational (SLR) play that stimulates others to engage in RT (Pellis & Pellis, 1983), others do not. For example, Syrian golden hamsters (*Mesocricetus auratus*) tend to be rather stolid creatures and, unlike rats, they never jump, run or pounce on one another (Pellis & Pellis, 1988). However, the complexity of the play is not correlated with the presence of SLR movements – hamsters have complex patterns of playful wrestling as do rats (Pellis & Pellis, 1987, 1988), and even though house mice have patterns of SLR play that are as exaggerated as those of rats (van Oortmerssen, 1971), their RT is limited to a simple pattern of approach-withdrawal (Pellis & Pasztor, 1999; Poole & Fish, 1975; Wolff, 1981). However, mice do show inter-animal coordination in some of their locomotor-rotational play (Terranova, Laviola, & Alleva, 1993; Laviola & Alleva, 1995), suggesting that even in a species with rudimentary social play, SLR movements may facilitate social engagement.

Carnivores. Among carnivores, self-handicapping and role reversals have only been systematically studied in domestic dogs. In a play group of 24 unrelated but familiar adult dogs, Bauer and Smuts (2007) found that in most playing pairs, one dog tended to adopt the offensive role significantly more often than the 50:50 rule would predict. The most dominant dog in the group hardly ever relinquished the offensive role during play, but many of the other dogs nevertheless sought her out for play, indicating that frequent role reversals are sometimes less important than other factors in determining play partner preferences. On the other hand, in a few dyads, roles were quite symmetric. This large variation across pairs may reflect differences in their relationship quality, with pairs that live together being more cooperative than those unfamiliar with one another. Also contrary to prediction, Bauer and Smuts (2007) found that younger dogs self-handicapped more than their older, more experienced partners did. Since younger dogs in general seem more eager to play than older dogs do, perhaps younger dogs self-handicapped more in order to induce older partners to play. This interpretation is consistent with the fact that younger animals also performed play signals more frequently than did their older partners (Bauer & Smuts, 2007). In a study of the development of play within litters, it was found that puppies developed specific play partner preferences which became more marked over time. Similar to adult dogs, young littermate pairs did not tend to follow the 50:50 rule, and their play became even more asymmetric with age (Ward, Bauer & Smuts, 2008; see also McNutt & Boggs, 1996 for similar findings in African wild dogs *Lycaon pictus*).

Nonhuman primates. Petrů et al. (2009) investigated the actions performed during play in five species of monkeys (*Semnopithecus entellus*, *Erythrocebus patas*, *Chlorocebus pygerythrus*, *Cercopithecus neglectus* and *Cercopithecus diana*). Of the 74 patterns characterized, 33 (45%) were judged to have a self-handicapping character. The self-handicapping patterns mostly involved making movements more physically demanding than necessary and exaggerating sensory input such as by performing somersaults and flips. Adult bonobos often engage in solitary energetic play sessions, where subjects challenge themselves in extremely acrobatic performances during which their vestibular apparatus is stimulated vigorously (Palagi & Paoli, 2007). At every age, bonobos love to climb, jump, dangle, and pirouette from supports in the environment while rapidly twisting. They often somersault on the ground covering several meters and alternate such performance with short and fast bouts of running (Palagi & Cordoni, 2012). Given that imitation can facilitate the social transmission of communicative signals (Miklósi, 1999), it is possible that the observation of another animal engaged in playful self-handicapping may increase the observer's motivation to play. Palagi (2008) tested the hypothesis of the social function of SLR play in adult bonobos. Bonobos use this communicatory tactic to elicit a playful response in the receiver: with about 50% of the solitary play sessions being followed by RT. Moreover, RT is more frequent when preceded by solitary play than by other self-directed behaviors, with pirouettes and somersaults being particularly frequent in the solitary play sessions directly preceding RT. However, care must be taken not to generalize from the findings of single species as the functions of such acrobatic movements and other postural maneuvers during RT may vary dramatically across species (Pellis, Pellis, Barrett & Henzi, 2014; Yanagi & Berman, 2014).

Humans. Children alternate between who is aggressing and who is the victim, with both partners self-handicapping (Pellegrini, 2009). For example, the “aggressor” may use exaggerated movements and open-handed hits and the “victim” may slow down to be caught or move into striking distance of the aggressor. In cases of adult-child play or in other unequal partnerships, the larger more competent and stronger partner typically self-handicaps (Pellegrini, 2009). Given that the amount of time spent in parent-offspring RT is positively correlated with children’s ability to translate bodily expressions into emotional states, it has been suggested that the ability to process play signals later with peers, may be rooted in the parent-offspring playful interactions (Parke, Cassidy, Burks, Carson & Boyum, 1992). Moreover, Pellegrini, Dupuis, and Smith (2007) posit that self-handicapping likely enhances the length of play bouts by increasing the players’ motivation and deterring boredom. Since RT gives opportunities to practice role reciprocation and self-handicapping, by playing with parents children can acquire an array of social strategies to engage in and maintain social interactions with peers (Pellegrini, 1993).

While relatively few studies have specifically focused on self-handicapping, restraint or role reversal in humans (Aldis, 1975; Smith & Boulton, 1990; Boulton, 1991), it seems likely that the use of self-handicapping during RT varies with age. For example, self-handicapping and restraining one’s strength appears to be less prominent in adolescence, an age at which RT provides a pathway to establish dominance relationships (Pellegrini, 2002). In infancy self-handicapping may promote proximity to peers which then may facilitate RT (Boulton, 1991), but data on such a linkage is wanting.

VI. LET’S SHARE OUR EMOTIONS! FACIAL AND BODY MIMICRY DURING PLAY

Matching one’s own behavior with that of others gives individuals the possibility to synchronize their activity with those of group members, to copy their behavior, and to place their behavioral activity in the appropriate context. The context of play, due to its plasticity, safety, and emotional involvement, provides a good substrate to investigate these mimicry processes. Experiencing others’ emotional states instantly allows an individual to foresee their playmates' intentions (Palagi, 2008) and fine-tune their motor sequences accordingly (Provine, 2000; Palagi & Mancini, 2011). So we can hypothesize that the ability to promptly respond with a mimicked action is an adaptive behavior.

Carnivores. Smuts (2007) argued that animals cooperating with one another in a "real" context (e.g., when resources or status are being contested) might negotiate their alliances first through synchronization of movements, which could occur during greetings, play or other contexts. Many different signals can be exchanged to negotiate cooperation, but they might not be honest. However, precise synchrony between different animals provides unmistakable evidence that two individuals are sufficiently invested in their relationship to be willing to expend time and effort to achieve such synchrony (Smuts, 2007). For example, in a bout of play in a pair of dogs, video analysis showed only 1/30th - 2/30th of a second occurred between the instant the first dog began to lower the forequarters and the second did so; in real time, the bows appeared perfectly synchronous (Smuts, 2007). While further study is needed, for present purposes we provisionally classify the play bow as an intentional, audience-dependent signal (*sensu* Horowitz, 2009) (Table 1).

Primates. In primates, different forms of imitation can be distinguished. Some forms are under voluntary and cognitive control, while others are involuntary, more linked to the emotions (Dimberg, Thunberg, & Elmehed, 2000; Iacoboni, 2009). For example, in humans, there are two possible responses to positive facial expressions: automatic responses (within 1.0 s), such as Duchenne smiles, and non-automatic responses (within 5.0 s), such as non-Duchenne smiles (Dimberg et al., 2000; Wild, Erb, Eyb, Bartels, & Grodd, 2003). The involuntary, automatic, mirroring and rapid response (e.g. the Duchenne smile, Table 1) given by the receiver is called Rapid Facial Mimicry (RFM) and can be distinguished from other forms of imitation (Iacoboni, 2009) by the rapidity of the matched reply. RFM plays an important role in emotional contagion by affecting one another's emotions or state of arousal (Davila-

Ross, Menzler, & Zimmermann, 2008; de Waal, 2008). There is evidence that facial mimicry in playful contexts correlates with the success of playful interactions. For example in chimpanzees, play bouts last more when the play face is bidirectionally performed by the two players (Waller & Dunbar, 2005). Moreover, social play sessions characterized by facial replication last longer than those sessions punctuated only by spontaneous laughter (Davila-Ross, Allcock, Thomas, & Bard, 2011). It seems, therefore, that the emotional synchronization through facial mimicry goes hand in hand with the cooperative side of social play. In humans, facial responsiveness requires a mechanism of "redirection of the sender's neural processing and perception toward one interactant and away from others" (Schmidt & Cohn, 2001, p. 14). For both sender and receiver, maintaining a social interaction and exchanging facial signals requires investment in focused attention to the partner, which, in turn, can lead to costs, such as lost opportunities to interact with others and scanning the environment for danger. Data on geladas supports this hypothesis, as the duration of play is positively correlated with RFM but not with delayed facial mimicry (Mancini et al., 2013a, Mancini, Ferrari, & Palagi, 2013b).

VII. MAKE A GESTURE TO TELL ME SOMETHING! GESTURES AS A COGNITIVE BREAKTHROUGH

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

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

In apes, gestures are narrowly defined as movements of hands, feet, or limbs with communicative function. One of the reasons to keep gestures apart from other forms of bodily communication (e.g., canine play bow) is that the two are neurologically distinct in both production and perception by others (Pollick & de Waal, 2007). A single brachio-manual gesture may communicate different messages depending on the social context in which the gesture is used (Tomasello & Call, 1997). This kind of dissociation between gesture and context has been observed in all great ape species, including humans (Bruner 1975; Call & Tomasello, 2007), and in all contexts, including play.

Different from other forms of communication more strictly linked to emotional components (i.e., vocalizations and facial expressions), gestures are mainly based on cognitive capacities and experience (Table 1). In the great apes, one of the proposed learning processes for improvement of the gestural repertoire is that of "ontogenetic ritualization", which is the capacity to create or invent new communicative signals by modifying pre-existing behavioral patterns (Tomasello & Call, 1997), so that a non-communicative pattern becomes communicative. For example, juvenile chimpanzees may initiate a play bout by slapping a potential playmate. If the receiver realizes that a play interaction often begins with the initiator raising an arm in preparation for slapping, the former may anticipate by responding playfully before actually receiving a slap. By noticing the anticipation of the receiver, the initiator may realize that the arm raising by itself is sufficient to elicit a playful response and thus, use that arm movement to elicit play (Tomasello, 1990). Although most evidence of ontogenetic ritualization is reported for immature subjects, it also appears plausible that adult apes are able to understand the cause-effect of a gesture, anticipate its function and, consequently, use a modified version of that gesture as a communicative signal (Palagi, 2008). There has been controversy, in recent literature, about the ontogeny of the intentional gestures of great apes (Hobaiter and Byrne, 2011a,b). Although the hypothesis of ontogenetic ritualization was able to account for the data reported in several studies, more recently doubts about it have arisen. Particularly, Genty, Breuer, Hobaiter, and Byrne (2009) comparing several gorilla populations, found no clear support for the hypothesis and detected no evidence that subjects had acquired novel gestures by imitation or other means of social transfer from conspecifics, such as population-specific differences in repertoire. They proposed that gorillas' gestures are species-typical as a result of genetic channeling in development, as with communicative signals of most other animals.

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

In all ape species, a great variety of gestures has been reported both in the wild and in captivity (Hobaiter & Byrne, 2011a,b, 2014). The gestural repertoire initially increases with age reaching the climax between the age of three-six years, and decreases again in adulthood (Tomasello & Call, 1997;

Call & Tomasello, 2007; Hobaiter & Byrne, 2011a), thus following the same ontogenetic trajectory as RT (Fagen, 1993). Even though there remain unresolved issues, the findings on great apes show that gestures are extensively used during play.

Gestural communication during playful interactions seems to be shaped also by the social structure of the species, with the highest frequency reported in the two *Pan* species (about 55% for bonobos, Pika et al., 2005; 47-70% for captive chimpanzees, Tomasello & Call, 1997; 40-63.4% for wild chimpanzees, Hobaiter & Byrne, 2011b), species that share a fission-fusion social system, characterized by fluid social interactions (Palagi, 2006). A slightly lower percentage (about 40%) has been reported for gorillas, which live in a one-male society (Fleagle, 1999), where adult relationships are limited to spatial proximity rather than affinitive closeness. The lowest percentage of gestures in the playful context has been observed in orangutans (about 22%) that live a more solitary life-style (Fleagle, 1999; van Schaik, 1999). In the two *Pan* species, playful interactions can frequently involve adults, whereas in gorillas and orangutans playful activities are more limited to immature subjects (Palagi et al., 2007). Considering the importance of the gestural repertoire for the playful context, social play in all its forms may represent an opportunity to train the communicative plasticity that is necessary to acquire gestures and to use them in an appropriate manner. Such cognitive plasticity in the use of gestural communication deserves much more attention by scholars of play and intentional communication systems. Some authors (Genty et al., 2009; Hobaiter & Byrne, 2011a) did not find any evidence of ontogenetic ritualization or social learning, leading them to conclude that, "naturally communicative gestures of great apes may, in their ontogeny, be more similar to primate vocalizations than has been realized." However, understanding the way apes and other primates communicate through gestures and how this capacity develops, becomes central when considering that it has been proposed that our ancestors' first linguistic expressions were in the gestural domain, more than in the vocal domain (Corballis, 2002). This hypothesis also seems to be supported by some neurological findings suggesting that human language probably has developed from gestural communication (Cantalupo & Hopkins, 2001; Hopkins, Russell, & Cantalupo, 2007).

VIII. CONCLUSIONS AND FURTHER DIRECTIONS

1) Play behavior, especially social play in the form of RT, due to its plasticity and versatility, is a complex phenomenon that challenges not only players but also scholars. Play may thus offer an avenue to study the precursors from which some forms of animal communication have evolved. Animal communication is certainly phylogenetically much older than play behavior, but play has provided a rich background for the development of flexibility in animal communication (Fagen, 1981, 1993).

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

3) We categorized signals used during play along two dimensions, each offering new insights and opportunities for cross-species comparisons.

(i) In the first dimension, it is recognized that some signals are based on patterns recruited from other functional contexts (see the left side of Table 1), others are patterns exclusively designed for play (see the right side of Table 1) and both these kinds of signals can serve similar functions. This theoretical categorization permits the delineation of, from a functional point of view, a common platform of play communication across different *taxa* thus favoring a comparative approach.

(ii) The second dimension is related to the proximate mechanisms that produces the signals. Some signals are driven by the emotions, and so relatively involuntary (lower part of Table 1) while others by cognition, and so relatively intentional (upper part of Table 1). Some lineages of animals have exaggerated the inter-play between the emotional and intentional aspects of play signals, yielding admixtures of communication that have led to very complex forms of RT. For example, rodents utilize both locomotor-rotational movements (intentional) and 50 kHz calls (emotional), both of which may serve to communicate the playful intentions of the participants. This blending of signals makes it difficult to distinguish intentional from non-intentional signals as from the receiver's perspective any signal that indicates the playful mood of the performer may be equally informative (Demuru et al., 2014). For instance, spontaneous laughter, which is the expression of a positive emotional state, can be read and cognitively utilized by the receiver to help manage the play session. If the laughter occurs during solitary play, the receiver can cognitively interpret the spontaneous, emotion-driven facial expression as a signal indicating the sender's propensity to engage in social play. The same may apply to self-handicapping and role reversal. They can be considered both intentional signals used strategically by animals to enhance play motivation of conspecifics and a form of emotionally self-rewarding action that can be interpreted by conspecifics as a signal of the benign intent of others.

4) Review of the play communication literature suggests that a sort of dualism between the emotional and intentional nature of a signal can be detected by applying a "shifting approach", whereby the emotional component of a signal can be revealed by analyzing its performance when the subject is alone (e.g., during solitary play) (Pellis & Pellis, 2011). The movements involved and their timing can be compared when the signal is performed during solitary play and when engaged in RT so as to reveal the performer's awareness of the presence of an audience (cognitive component) (Palagi, 2008; Yanagi & Berman, 2014). When the cognitive component comes into play, the signal can be enriched by new

elements (exaggeration, amplification, long-lasting performance, repetition) that improve its detection by a potential receiver.

5) Future studies need to bring together two avenues of investigation. First, as seen from the comparative survey, few species have been studied with the intensity needed to characterize the range and type of play signals used in their repertoire, much less the contexts in which different signals may be used. Given that much of what we know is derived from carnivores, primates and rodents, and that these represent highly diverse Orders, it seems only reasonable to recommend that a broader range of species in these, and possibly other, mammalian be added to the comparative data set. The independent radiations of marsupial mammals and birds may be particularly useful to test hypotheses derived from the currently limited data on placental mammals. Also, as shown in this review, there is considerable variation across species and lineages of species as to how complex the play can be, and, in part, these variations are likely to depend on the tactics used to ensure that interactions maintain the minimum degree of reciprocity needed for them to remain playful. Aside from these empirical requirements, the emerging comparative data set needs to be integrated with novel theoretical approaches. A deeper understanding about the functions of reciprocity, synchronicity and incongruity in interactions could be provided by mathematical modeling (e.g., game theory, Fagen, 1981; Dugatkin & Bekoff, 2003), which, in turn, could alert researchers to look for variations in behavior that are currently not considered. A better understanding about the range and use of play signals and how these are used to navigate the demands of reciprocity during play could then be used as a basis for analyses involving the methods of comparative biology to determine the factors that have promoted the evolution of signals along the dimensions that we have delineated (Table 1). Social systems that involve highly nuanced social relationships and expanded cognitive capacity (likely reflected in expansion of frontal areas of the cortex) seem to be promising factors to explore in this regard.

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Table legend

Table 1 - The figure shows the categorization of communicative signals commonly used in Rough-and-Tumble play. The table is organized according to two theoretical dimensions: signal specificity (signals designed for play - right side - and signals recruited from other functional contexts - left side) and proximate causes of signals (emotionally driven signals - lower part - and cognitively driven signals - upper part).

INTENTIONAL SIGNALS

PATTERNS RECRUITED FROM CONTEXTS OTHER PLAY

PATTERNS EXCLUSIVE TO PLAY

FACIAL EXPRESSIONS

Non-human primates: lipsmacking (macaques, baboons, geladas), bared teeth (macaques).

Humans: Non-Duchenne smile

BEHAVIORAL PATTERNS RECRUITED FROM OTHER CONTEXTS AND USED IN ROLE REVERSAL and SELF-HANDICAPPING

Carnivores: Inhibited bites (dogs, bears, hyenas) and clawing (black bears)

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).

BEHAVIORAL PATTERNS RECRUITED FROM OTHER CONTEXTS USED TO SOLICITE 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

FACIAL EXPRESSIONS

Non-human primates: Full play face in adult geladas. Play faces in juvenile chimpanzees in presence of a particular audience (e.g. the mother of the younger playmate).

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.

BODY POSTURES AND MOVEMENTS EXCLUSIVE OF PLAYFUL CONTEXT

Canids: play bow

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

BODY POSTURES AND MOVEMENTS

Canids: Play rolling and squirming during solitary play

FACIAL EXPRESSIONS

Non-human primates: Playful facial displays performed in the middle of a 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 context (non-Duchenne smile, see the upper-left quadrant)

BODY POSTURES AND MOVEMENTS

Rodents and Primates: Locomotor-rotational movements during solitary play

Primates: Head rotation in langur solitary play

EMOTIONAL SIGNALS