

RESEARCH ARTICLE

Directedness and engagement in chimpanzee vocal ontogeny

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Abstract

Directedness and engagement during pre-verbal vocal communication play a major role in language development. What was their role in the evolution of language? This question invites us to examine these behaviours in chimpanzee vocal ontogeny. We collected observational data on infant ($N = 15$) and juvenile ($N = 13$) chimpanzees at Chimfunshi Wildlife Orphanage, Zambia. We examined the impact of age and vocalization type (grunts, whimpers, laughs and screams) on directed cues (gaze directedness and face directedness) and engagement (mutual face directedness) during vocal communication. We also assessed the impact of directed cues and engagement on social interactions by coding the behaviour of social partners before, during and after a vocalisation, and examining whether they contingently changed their behaviour in response to the vocalisation if it was directed or if engagement occurred. We found that face directed vocalisations showed a general increase during ontogeny and we observed call-type dependent effects of age for mutual face directedness. Only face directed vocalisations were significantly predictive of behavioural responses in social partners. We conclude that like young humans, young chimpanzees routinely exhibit directed behaviours and engagement during vocal communication. This social competency improves during ontogeny and benefits individuals by increasing the chances of eliciting behavioural responses from social partners. Directedness and engagement likely provide a foundation for language phylogenetically, as well as ontogenetically.

KEYWORDS

chimpanzee, communication, directedness, engagement, ontogeny, vocalisation

Research Highlights

- We show that directedness and engagement routinely occur during early chimpanzee vocalisations.
- Directedness increases throughout chimpanzee vocal ontogeny, similar to human infants.
- Directedness enhances social partner responsiveness, demonstrating a direct benefit to this style of communication.

Guillaume Dezecache and Marina Davila-Ross contributed equally to this study.

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- Directedness and engagement could provide a route towards language phylogenetically as well as ontogenetically.

1 | INTRODUCTION

Directedness of communicative acts (i.e., selection of a specific social target through cues such as gaze direction and facial orientation) and engagement during communication (i.e., mutual attention while communicating) are known to play an important role in language development (Donnellan et al., 2020; Lavelli & Fogel, 2005). Suggested reasons for this include that directedness and engagement during communication facilitate the expression of intentions (Harding, 1982) which in turn enhances the initiation of dyadic interactions (Nicely et al., 1999). Although, such forms of communication may not necessarily qualify as intentional and may instead be strategies employed to enhance the influence of a signal upon others through simple attentional processes (see Rendall et al., 2009)

The role of directed vocal communication in early social interaction is demonstrated by studies using the still face paradigm, which have shown that, by 5 months of age, human infants seem to use directed vocalisations to capture the attention of an inattentive social partner (Delgado et al., 2002; Goldstein et al., 2009). However, studies that sampled a wider range of ages, from 4 to 10 months of age, found that infants did not direct their vocalisations towards others above chance level until 10 months of age, suggesting directed vocal behaviour is a social competence that improves during ontogeny (D'Odorico & Casibba, 1995; D'Odorico et al., 1997). This may be related to maternal responsiveness, since infants whose mothers are more responsive to directed vocal behaviour at 8 months show significantly more directed vocal behaviour at 14 months (Gros-Louis et al., 2014). Among 11-month-old human infants, directed vocalisations are also more likely to elicit responses from caregivers than non-directed vocalisations, demonstrating that directed vocal behaviour is effective at engaging social partners (Donnellan et al., 2020). Moreover, infants who show more directed vocal behaviour at this age have been found to have a greater expressive vocabulary size at 2 years of age (Donnellan et al., 2020), demonstrating a direct relationship with language.

The engagement between infants and social partners established by directed communicative acts also impacts human communicative development. Engagement is important during early ontogeny because it provides a means of understanding others' psychological states (Reddy, 2019), and while engagement may take many forms (i.e., tactile engagement, auditory engagement), a particularly common form early in human ontogeny is visual engagement as indicated by mutual gaze (Reddy, 2010). As early as 2 months of age, vocalisations and facial expressions are routinely produced during mutual gaze (Lavelli & Fogel, 2005), suggesting infants harness mutual engagement as an opportunity to communicate. This is further supported by the observation that infants aged 4–24 weeks produce vocalisations more frequently

when participating in mutual engagement than when not (Hsu & Fogel, 2001) and by 4 months of age, infants show increased activity in the temporal and prefrontal cortex during mutual gaze (Grossmann et al., 2008) as well as increased neural synchronisation between infants and social partners during mutual gaze at 8 months (Leong et al., 2017). At this age, the vocalisations produced during mutual gaze mostly express positive affect (Colonnese et al., 2012), which has been observed to encourage caregivers to continue their interactions with infants (Oller et al., 2013). Such forms of engagement have also been found to impact the diversity of vocal production patterns among infants (Franklin et al., 2014), suggesting an important role in vocal ontogeny. While directedness and engagement appear to play an important role in human communicative ontogeny, the role of such behaviours in the phylogeny of human language and communication is less known.

In the present study, we aimed to assess 'directed' vocal communication and visual engagement during vocal communication throughout chimpanzee ontogeny, using approaches (i.e., measuring subjects' gaze direction and facial orientation towards social partners, as well as mutual face directedness) that more closely align with those used in the human infant literature (e.g., Donnellan et al., 2020; Long et al., 2020; Northrup & Iverson, 2020) than those previously used in primatological studies (e.g., Laporte & Zuberbühler, 2011). Indeed, there is good reason to expect such visual cues to play a role in chimpanzee communication. Aspects of primate eye-morphology that are known to be important during communication, such as width of the iris, strongly correlate with social complexity among primates (Kobayashi & Hashiya, 2011). Since chimpanzee social structure has been shown to outstrip that of many other primate species regarding complexity (Aureli & Schino, 2019), this suggests that gaze-related behaviours likely play an important role in chimpanzee communication. Studies of mother-infant interactions in chimpanzees have shown that mother-infant dyads routinely participate in mutual gaze (Bard, 1994) and there are group level differences in this pattern which may relate to the environment of different populations (Bard et al., 2005). To our knowledge, however, there are no studies of the relationship between mutual gaze and vocal communication in chimpanzees.

Directedness has played an important role in research on ape gestural communication (see Krause et al., 2018; Tomasello & Call, 2019). However, a comparably small number of studies have examined whether non-human primate vocalisations are 'directed' to specific individuals. Seyfarth and Cheney (2018) reported that baboons direct calls to specific individuals. For example, baboon grunts are usually directed towards lower ranking individuals, and behavioural cues such as gaze can be used to ascertain who the target of a call is, indicating directedness may also play an important role in primate vocal communication.



The evidence on directed vocal communication among great apes is more indirect inasmuch as behavioural cues of directedness have seldom been studied. Instead, playback experiments are typically used. For example, playback experiments with chimpanzees and bonobos show that individuals selectively produce vocalisations in response to hearing vocalisations from specific individuals (i.e., those who are high ranking: Genty et al., 2014; Schel et al., 2013) and selectively vocalise in response to conspecifics who are unaware of the presence of a predator (Crockford et al., 2012, 2017). These studies hint at the possibility of directed vocal communication in great apes. However, since these studies differ markedly in their methodology from studies of human infants, the implications of such studies for our understanding of the evolutionary origins of language remain unclear.

With regard to ontogeny, Laporte and Zuberbühler (2011) observed the grunts of infant, juvenile and sub-adult chimpanzees produced in reaction to the approach of conspecifics, which the authors thereby considered to be directed. Notably, this approach stands in contrast to the human infant literature (e.g., Donnellan et al., 2020; Long et al., 2020; Northrup & Iverson, 2020) wherein vocalisations are considered to be directed on the basis of additional cues produced by the signaller such as gaze direction and facial orientation. Nonetheless, like human infants, grunts began to be 'directed' towards others at approximately 2 months of age. Later in ontogeny (i.e., during the juvenile and sub-adult periods), however, grunts were 'directed' towards others less often, but increased in the specificity of who grunts were 'directed towards' – primarily dominant males. Interestingly, the authors also reported never observing vocal communication during mutual gaze. Dezechache et al. (2019) studied the role of gaze in the ontogeny of chimpanzee alarm calls. The authors found alarm calling increased with age, but gaze alternations between conspecifics and a predatory stimulus during alarm calls were common at all ages, suggesting alarm call ontogeny may be influenced by early gaze alternations. While relevant, gaze alternations primarily indicate reference or monitoring rather than social directedness per se, and in human infants have primarily been studied in relation to referential gesturing rather than vocal ontogeny (e.g., Cochet & Vauclair, 2010), leaving the relationship between gaze behaviours during chimpanzee and human vocal ontogeny unclear. Notably, both studies focused on a single call type, whereas the human infant literature shows call types differ in their directedness (see Oller et al., 2013 [Supplementary materials](#)), highlighting the importance of investigations across call types. No study of non-human primate vocal production has yet examined the ontogeny of directed behaviours during vocal communication, such as gaze directedness, and more notably face directedness and mutual gaze, which play a particularly important role in human communicative acts (Gómez, 1996; Moore, 2016). Consequently, it is unclear whether this is a social competency that improves in ontogeny as in the human case (D'Odorico & Cassibba, 1995; D'Odorico et al., 1997). Furthermore, while in humans, directed communicative behaviours are more likely to elicit responses from social partners (Donnellan et al., 2020), no studies of chimpanzees have examined the impact of directed communicative behaviours on social interactions.

Since very little is known about the ontogeny of directedness and engagement during chimpanzee vocal ontogeny, and what is known is limited to a small number of call types (primarily grunts), in this study we assessed directed vocal communication and engagement throughout the vocal repertoire of semi-wild infant and juvenile chimpanzees. In particular, we aimed to assess what cues of directedness are present during vocalisations (i.e., gaze direction and facial orientation), how often directedness and engagement occur during vocal communication in chimpanzee ontogeny, and the impact of directedness and engagement during communication on social interactions. Achieving these aims will fill a crucial gap in our understanding of the evolutionary origins of language by elucidating whether directedness and engagement play a role in chimpanzee vocal ontogeny as is observed in humans.

2 | METHOD

2.1 | Subjects and study site

Subjects were infant ($N = 15$) and juvenile ($N = 13$) chimpanzees housed at Chimfunshi Wildlife Orphanage (CWO). Infant ages ranged between 0 and 4 years of age ($M = 1.13$, \pm SD = 1.14). Juvenile ages ranged from 4 to 10 years of age ($M = 7.07$, \pm SD = 3.82). Typical infant characteristics include riding either ventrally or dorsally with the mother and breast-feeding from the mother. Typical juvenile characteristics include no longer riding with the mother either ventrally or dorsally, less reliance on breast feeding from the mother, and more independence from the mother (see Laporte & Zuberbühler, 2011; Reynolds, 2005; van de Rijt-Plooi & Plooi, 1987). All subjects were raised by their mothers during infancy, and all infant subjects still lived with their biological mothers. Three juveniles (one 5-year-old male, one 10-year-old male and one 8-year-old female) did not live with their mothers due to fatalities that occurred in years prior to the present study. While the majority of chimpanzees at CWO are rescued from adverse circumstances, such as the pet trade, all subjects in the present study were born in captivity. However, the majority (78%) of their mothers were originally wild. Chimpanzees housed at CWO belong to a mixture of chimpanzee sub-species, including *Pan troglodytes troglodytes* and *Pan troglodytes schweinfurthii*. Each subject belongs to one of four mixed-sex colonies that comprise between 10 and 52 members. For a further breakdown of the study population see [Table 1](#).

Each subject was housed in one of four outdoor miombo forest enclosures. Miombo woodland is the habitat of many wild chimpanzee populations (Schoeninger et al., 1999). Enclosure sizes were 190 (group 1), 160 (group 2), 47 (group 3) and 62 (group 4) acres. Here, chimpanzees are fed once daily at approximately 12 p.m., and some chimpanzees are fed indoors. Beyond this, chimpanzees of CWO forage on naturally fruiting trees. The enclosures and group sizes are large enough that fission fusion social dynamics take place as well as regular territory patrols. At night, all chimpanzees sleep outside and many show nesting behaviours.

**TABLE 1** Overview of subject characteristics including developmental stage, age, sex, and group membership

Developmental stage	Age (Years)	Sex	Group
Infant	0	Males (2); Females (3)	1, 2, 3
	1	Males (1); Females (1)	1, 2
	2	Males (3); Females (3)	1, 2
	3	Males (1); Females (1)	1, 2
Juvenile	4	Males (0); Females (2)	1, 2
	5	Males (1); Females (1)	2, 3
	6	Males (3); Females (1)	1, 2
	7	Males (1); Females (0)	3
	8	Males (1); Females (1)	2, 3
	9	Males (1); Females (0)	4
	10	Males (1); Females (0)	3

2.2 | Data collection

Video and audio recordings were collected between 7 a.m. and 6 p.m. from June 2018 to October 2018 (excluding 12 p.m.–1 p.m. when daily feeding occurred) using a Sony CX405 Handycam with a Sennheiser ME66 directional microphone attached. Recordings were collected only when the subjects were outdoors, and the recordist was within 2–10 m of the subject. The main approach in collecting recordings was to use a 5-min focal sampling method that allowed us to have equal representation of the sample in this study. These focal recordings for each subject were collected in a new order each day determined by using a random number generator. However, due to the large size of the enclosures and the dense forest inside them, subjects were often not visible. For efficiency, we therefore decided to wait for 5 min to observe a subject. If the subject was not visible, we then recorded the visible chimpanzee who was next highest on the focal recording list that day. It was attempted to obtain two such focal recordings on a subject in a single day – one in the morning (before 12 p.m.) and one in the afternoon (after 1 p.m.). Six hundred and fifty 5-min focal recordings were collected overall. In addition, there were 44 recordings that were incomplete as the subjects left the view of the camera for more than 30 s and could therefore no longer be seen and identified as the potential caller. Furthermore, when there were no visible subjects where 5-min focal recordings could be taken for that day, the subjects were recorded ad libitum. Seventy-nine ad libitum recordings were taken. These additional recordings were also included in the analysis of this study in order to increase the overall number of calls.

Overall, between 15 and 51 focal recordings were collected per subject, meaning focal observation time ranged between 1.24 and 4.25 h of recording per subject (Infants: $M = 2.72 \pm SD = 0.96$; Juveniles: $M = 3.43 \pm SD = 0.04$). The total duration of ad libitum recordings per subject ranged between 0.03 and 3.52 h (Infants: $M = 0.81 \pm SD = 0.79$; Juveniles: $M = 0.18 \pm SD = 0.15$). The total duration of incomplete focal recordings ranged between 0.20 and 1.27 h per subject (Infants: $M = 0.70 \pm SD = 0.33$; Juveniles: $M = 0.55 \pm SD = 0.28$). Overall, total observation time ranged between 1.73 and 5.45 h per subject (Infants:

$M = 4.19 \pm SD = 1.31$; Juveniles: $M = 4.16 \pm SD = 0.53$). For a full breakdown per subject see supplementary methods Table S1.

2.3 | Identifying calls

The coded unit of vocal behaviour was the call type, which is a broad category of calls (e.g., grunts) which may contain distinct variants (e.g., food grunt, pant grunt). Call types were chosen because there is wide agreement regarding the call types produced by immature chimpanzees (Goodall, 1990; Plooi, 1984; Slocombe & Zuberbühler, 2010) but whether immature chimpanzees exhibit distinct subtypes (i.e., food grunts, pant grunts) is currently unclear due to a lack of systematic study. Moreover, in a recent study of infant and juvenile vocal behaviour (Taylor et al., 2021), we demonstrated the validity of these call types by using unsupervised machine learning techniques to show that based on acoustic information alone and without call labels, a clustering algorithm grouped the majority of each call type into distinct call clusters, suggesting call types can be reliably distinguished from one another in infants and juveniles.

Calls could be comprised of a single call element (i.e., one call), or a series of call elements otherwise known as a call 'bout'. Seven hundred and sixty-eight calls were identified in total. Bouts were also included in order to avoid pseudo-replication of calls (i.e., a rapid series of calls are likely not independent from one another), which is problematic from a statistical point of view in the analysis of animal calls (see Waller et al., 2013). A call was independent from a preceding call if it either occurred >5 s from the preceding call, or, if the call type in a series of calls changed, similar to previous studies of early chimpanzee vocal behaviour (see Davila-Ross et al., 2009; Dezechache et al., 2020). The call types included grunts ($N = 382$), whimpers ($N = 147$), laughter ($N = 139$), screams ($N = 41$), hoo calls ($N = 41$), barks ($N = 8$), squeaks ($N = 6$) and pant hoots ($N = 4$). There was sufficient data only for analyses of grunts, whimpers, laughs and screams. Hoo calls were not included because directedness could only be coded for just 21 calls and only five of these were observed among infants, meaning there was

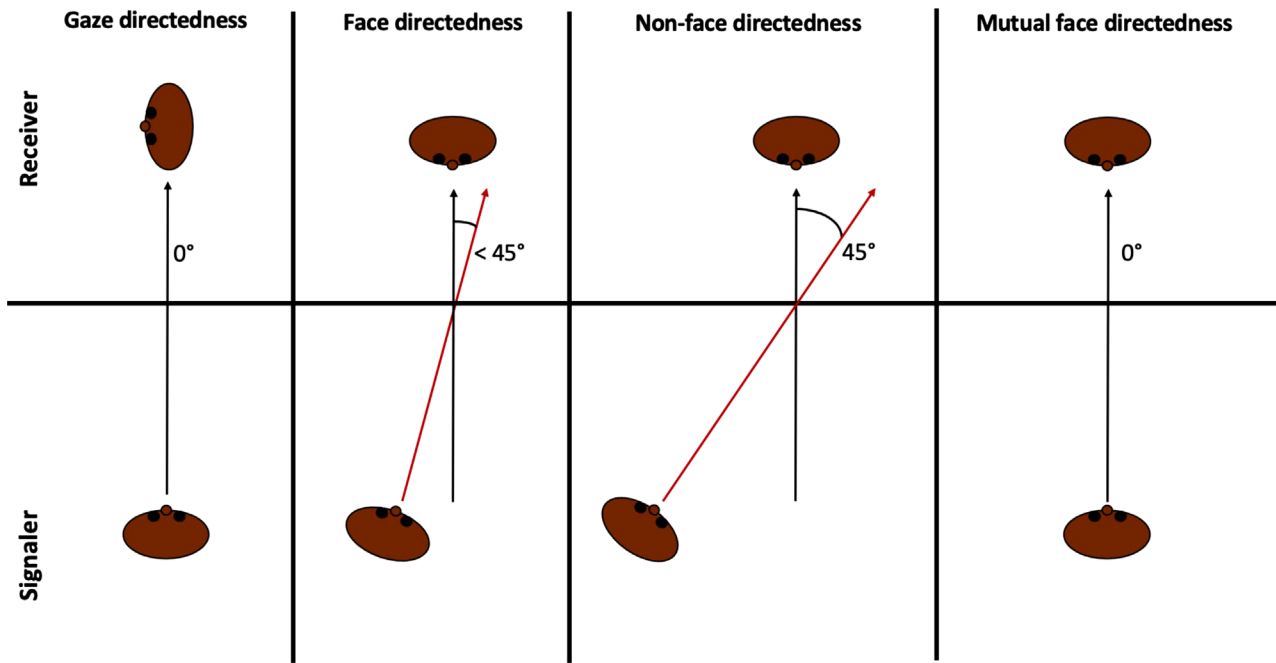


FIGURE 1 Illustrations of directedness coding. In all panels, the black arrow corresponds to the 0° reference point. Red arrows indicate deviation from the 0° reference point in the signaller's gaze direction. Gaze directed vocalisation (definition 1) is illustrated in the left-hand panel. Face directed vocalisation and non-face directed vocalisation (definition 2) are illustrated in the two centre panels. Mutual face directedness (definition 3) is illustrated in the right-hand panel. Actual coding was based on observer judgements since it was not possible to systematically evaluate angles due to variation in relative positions between subject, social partner, and observer in a 3-dimensional space.

insufficient data to test for an effect of ontogeny. Pant-hoots were also not included because they are a combination of call types rather than a single call type (Fedurek et al., 2013). Calls were identified based on auditory cues followed by systematic visual inspection of spectrograms according to the definitions used in Taylor et al. (2021). An inter-rater reliability test was performed on 20% of the total identified calls, and Cohen's Kappa revealed a good (see Cohen, 1960) level of reliability ($K = 0.75$).

2.4 | Directedness and engagement coding

Directedness and engagement were coded while a subject vocalised. A call was coded as directed or during engagement if at any time throughout its duration it met criteria for directedness or engagement. There was no significant difference in total observed duration between call types (Friedman test: $\chi^2(4) = 2.314$, $N = 7$, $p = 0.509$). There was also no statistically significant correlation between age and total duration observed vocalising (Spearman's Rho: $r_s(11) = 0.490$, $N = 28$, $p = 0.149$).

2.5 | Directedness and engagement

Three different types of directedness were studied. Two, 'gaze directedness' and 'face directedness', pertain to directedness cues produced by the subject. The third, which we term 'mutual face directedness'

refers to where the social partners' and subjects' faces are oriented towards one another; it was our indicator of visual mutual engagement. Each type of directedness was defined as follows:

(1) Subjects' gaze is directed towards a conspecific while the subjects' body is orientated towards the conspecific (hereafter 'gaze directed'). Note, the social partner did not have to be oriented towards the subject for the vocalisation to qualify as gaze directed (see Figure 1).

(2) Subjects' face is orientated towards the face of a conspecific while the subjects' body is orientated towards the conspecific (hereafter 'face directed'). To be considered face directed, the subjects' face must have been judged to be $<45^\circ$ of the social partner's face (see Figure 1). Thus, face directedness differed from gaze directedness in that the social partner could not be facing away from the subject when a vocalisation was face directed, meaning face directed vocalisations are a subset of gaze directed vocalisations.

Although our directedness criterion differs from that used in human infant studies (e.g., Donnellan et al., 2020) wherein gaze is usually not considered directed unless the infant is looking directly at the face or eyes of the caregiver (meaning, for example, our criterion for gaze directedness may not be considered directed in some human infant studies), such criterion have been previously used with success in studies of animal behaviour wherein observation conditions are considerably more challenging and consequently evaluating gaze direction at the level of specificity attainable in human infant studies is not possible (e.g., Davila-Ross et al., 2011; Palagi et al., 2019).



TABLE 2 Categories of social partner behaviour towards subjects and behaviours that belong to each category. See Plooij (1984) for definitions of behaviours

Category	Behaviours toward subject
Feeding offspring	Food sharing, breast feeding
Protecting	Defending subject, gathering subject
Comforting	Cradling, patting, embracing, bite-kissing, holding hand, extending hand
Playing	Playfully wrestling, tickling
Grooming	Grooming, inspecting
Approach	Approaching subject
Travel	Lowering back for subject to climb on, following subject, carrying subject
Avoidance	Avoiding subject, leaving subject, or breaking contact with subject outside of play
Preventing breastfeeding	Covering nipple (mothers only)
Threat	Arm raising gesture, biting at (outside of play), dominance displays
Taking	Taking or pulling objects in subjects' possession
Causing discomfort	Pulling, slapping, hitting, dragging, pulling hair, pushing subject (outside of play)

Definitions 1 and 2 are important distinctions firstly because chimpanzees are known to be sensitive to both gaze and face orientation of others during communication (e.g., Kaminski et al., 2004). Secondly, following definition 1, subjects may not necessarily be within the conspecifics line of sight during gaze directed vocalisations, meaning the conspecifics may not realise they are the target of a directed call, making definition 2 important to include. Finally, definition 2 is also important because the development of face-to-face vocal communication is a key milestone in human vocal development (Fogel, 1993; Jaffe & Feldstein, 1970; Oller, 2004). If the face of the subject was not visible (i.e., the subject was out of view or facing the opposite direction to the recordist), directedness was not coded.

(3) The third type of directedness was 'mutual face directedness'. Directed vocal behaviour is an essential pre-requisite for engaging others during communication when engagement is defined as mutual gaze (Bard et al., 2005) during communication. In this study, mutual face directedness was considered to occur during communication if the subject's face was orientated towards the face of a social partner and the face of the social partner was orientated towards the face of the subject at the same time while the subject was vocalising (see Figure 1). Given that face directedness is a pre-requisite for mutual face directedness, mutual face directed vocalisations were a subset of face directed vocalisations. To be considered as face orientated for both subjects and social partners, both individuals' faces must have been judged to be <45° of one another. If the face of the subject or social partner was not visible (i.e., the subject or social partner was out of view, or facing the opposite direction to the recordist), mutual face directedness was not coded.

All coding of directedness was binary – either the call was directed or not. A high level of intra-rater reliability was achieved based on 20% of the full dataset (Gaze directed, $K = 0.81$; Face directed, $K = 0.84$; Mutual face directedness $K = 0.90$). The intra-rater reliability coding occurred 9 months after the original coding was completed.

2.6 | Social partner behaviour and responses

The social partner referred to the individual(s) that the subject was interacting with while vocalising. When calls were directed, this was the individual the call was directed towards. The behaviour of the social partner was coded 4 s before the vocalisation, during the vocalisation, and 4 s after the vocalisation. This time frame was chosen because studies of chimpanzee infants that examined mothers behavioural responses to their infants vocalisations used a similar time frame (e.g., Dezechache et al., 2020). All observed behaviours were coded using the ethogram developed by Plooij (1984). See Table 2 for behaviour categories and the behaviours that comprised each category. Behavioural responses in a social partner were defined as when a social partner either stopped a category of behaviour or started showing a new category of behaviour during or after the subjects' vocalisation was produced. Notably, behavioural categories were not mutually exclusive (i.e., a social partner may show both protecting and comforting behaviours during a vocalisation), meaning if only one category stopped or was introduced while another was consistent throughout, the social partner would still be considered to have changed their behaviour. All coded behaviours were directed towards the subject. The social partners' behavioural response (i.e., change vs. continue based on the categories of behaviour shown in Table 2) was intra-rater reliability tested using Cohen's Kappa, which showed an excellent degree of reliability was achieved based on 20% of the overall dataset ($K = 0.88$). The intra-rater reliability coding occurred 9 months after the original coding took place.

2.7 | Statistical analysis

Since our independent variable was binary, generalized linear mixed models with a binomial error structure and a log link function were used to examine the impact of age (in years) and call type



(grunts, whimpers, laughs and screams) on directedness and engagement. Three models were built with identical fixed effects and random effects structure, but different dependent variables that reflect different aspects of directedness and engagement. In one model the dependent variable was gaze directedness, in another the dependent variable was face directedness, and in the third, the dependent variable was mutual face directedness (see 'directedness and engagement coding' above for definitions). In all models the fixed effects were age and call type. Since there were individual differences in the number of observations, ID was used as a random effect. Additionally, previous studies have shown different colonies of the study population significantly differ in aspects of their social behaviour such as social tolerance (see van Leeuwen et al., 2018) which is measured using social proximity and therefore might limit an individuals' ability to exhibit directed communicative behaviours. Consequently, we included colony as a random effect. Since individuals are nested within different enclosures, a nested random effects structure was used. Initially, sex was also included as a random effect as previous studies show young male and female chimpanzees are socialised differently (see Lonsdorf et al., 2014). However, when sex was included as a random effect, models were unable to converge because there was zero variance in parameter estimates for sex. Consequently, sex was not included as a random effect in any model. All models successfully converged and took the following form: Directedness as dependent variable, the interaction of Age in Years and Call Type as fixed effect, and the nested random effect of ID nested in Enclosure Number. This model was compared to both a reduced model without the main interaction and a null (intercept and random factor only) model. We used likelihood ratio tests to compare models and calculated conditional R squared values to measure the difference in explained variance between models. If there was no significant difference between models, the simpler model (i.e., the model with fewer predictors) was preferred since this suggests the more complex model does not add any predictive power. Wald Chi-Square tests were used to test whether each parameter in the final model was significant.

To assess the impact of directedness on social interactions, we used three generalized linear mixed models with a binomial error structure and a log link function. Each model had the same dependent variable – whether or not a social partner changed their behaviour in response to a vocalisation. Each model had a single fixed effect which differed between each model. The fixed effects were either gaze directedness, face directedness or mutual face directedness. Two random effects were used. One random effect was ID, due to an uneven number of observations per individual. Originally this was nested within enclosure as per the above models but enclosure was removed due to zero-variance in parameter estimates when included which prevented model convergence. The second was call type due to differences in responsiveness to different call types, for instance, mothers show high levels of responsiveness to infant whimpers (see Dezechache et al., 2020). Social partner ID was originally included as a random effect. However, this was removed from all models built to predict social partner responsiveness due to zero variance in parameter estimates, which prevented model convergence. All models converged and took

the following form: Social partners' response as dependent variable, Directedness or Engagement as fixed effect, and ID and Call Type as random effects. These were compared to a null (intercept plus random effects only) model. Likelihood ratio tests were employed to compare models and conditional R squared was calculated to measure the difference in explained variance between models. If there was no significant difference between models, the simpler model (i.e., the model with fewer predictors) was preferred since this suggests the more complex model does not add any predictive power. Wald Chi-Square tests were used to test whether each parameter in the final model was significant.

All generalised linear mixed models were run in R V3.5.2 (R Core Team, 2016) using the lme4 package V1.1.23 (Bates et al., 2007) to fit the models. The emmeans package V1.5.1 (Lenth et al., 2018) was used to perform post-hoc comparisons with Tukey comparisons in the best fitting model. The MuMIn package V1.43.17 (Barton & Barton, 2015) was used to calculate conditional R squared values. All models were also subject to checks (i.e., evaluation of multi-collinearity, overdispersion and linearity between continuous predictors and the logit of the dependent variable) which showed the models were a good fit to the data and the data did not violate assumptions of the models.

3 | RESULTS

3.1 | Ontogeny of directedness and engagement during vocal communication

Fifty-six percent of all vocalisations were directed towards a conspecific using gaze. Among the 56% of gaze directed vocalisations, 34% of all vocalisations were directed towards the face of a conspecific. Among the 34% of face directed vocalisations, mutual face directedness occurred during 17% of all vocalisations. Importantly, these estimates include vocalisations produced when the social partner was both visible and not visible, making them a relatively conservative estimate of the proportion of vocalisations produced with cues of directedness and engagement. Gaze directedness, face directedness and mutual face directedness during grunts and whimpers were all observed within the first month of life, with directedness and mutual face directedness for all other call types being observable within the first 2 years. Raw values for all models are shown in supplementary results A, Tables S2–S4.

3.2 | Directedness

A full model wherein gaze directedness was predicted by an interaction between age and call type was significantly different from a null model (LRT: $\chi^2_7 = 27.136$, $p < 0.001$, $R^2_c = 0.180$). However, the full model was not significantly different from a reduced model including age and call type as fixed effects with no interaction between them (LRT: $\chi^2_3 = 5.433$, $p = 0.143$). As such, the reduced model was preferred. In this reduced model, there was no significant effect of age on gaze directedness during vocal communication. However, there was

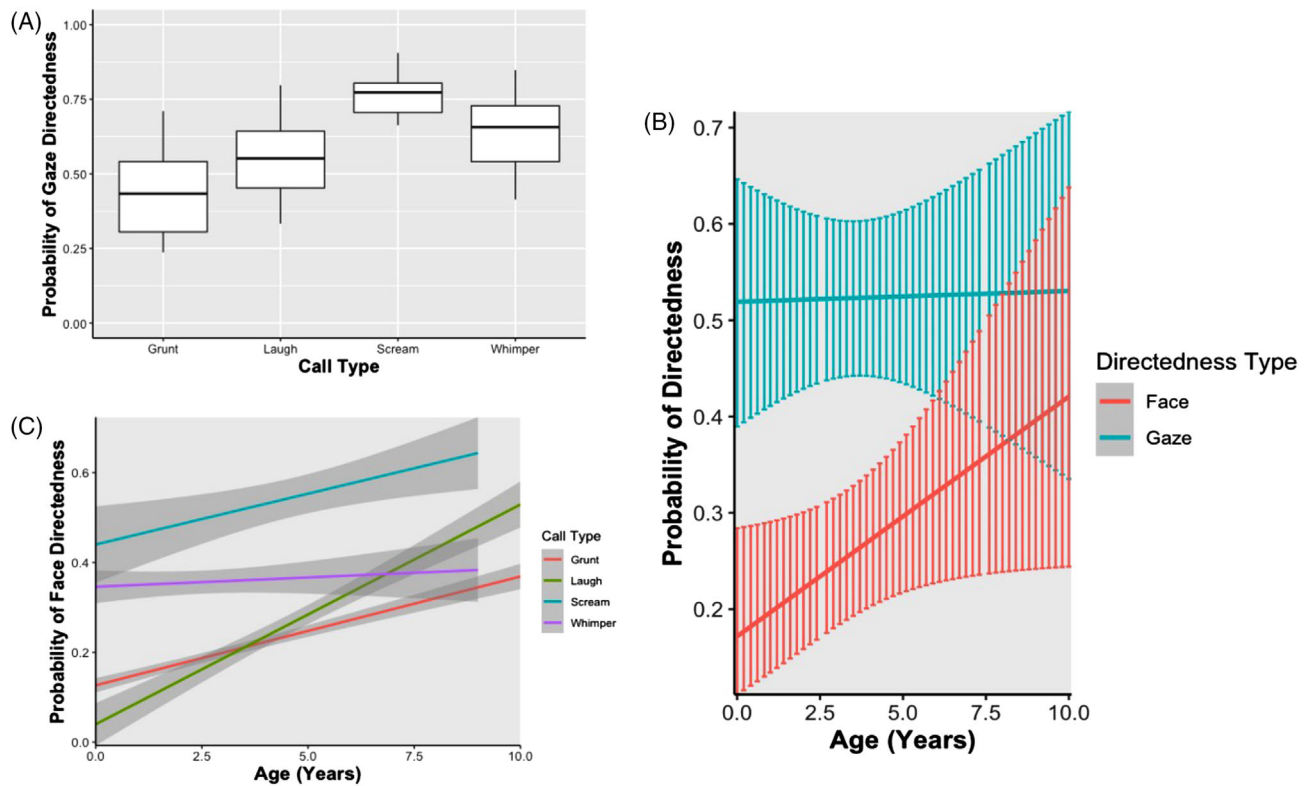


FIGURE 2 Main effects and interactions of models using age and call type as predictors of gaze directedness (a) and face directedness (c). Grey areas indicate 95% confidence intervals. Furthermore, the age effect for face directedness is shown compared to the lack of an age effect for gaze directedness (b). Blue and red bars indicate 95% confidence intervals for gaze and face directedness, respectively.

a significant effect of call type (Wald Chi-Square test: $\chi^2_3 = 5.433$, $p < 0.001$), with gaze directedness during communication being significantly more likely for screams ($\beta = 1.508$, $SE = 0.451$, $Z = 3.343$, $p = 0.004$), and whimpers ($\beta = 0.821$, $SE = 0.244$, $Z = 3.363$, $p = 0.004$), compared to grunts (Figure 2a). All model values for the preferred model are shown in supplementary results B Table S6.

A full model wherein face directedness was predicted by an interaction between age and call type was significantly different from a null model (LRT: $\chi^2_7 = 25.919$, $p < 0.001$, $R^2_c = 0.230$). The full model was also significantly different from a reduced model wherein face directedness was predicted by age and call type with no interaction (LRT: $\chi^2_3 = 8.877$, $p = 0.030$). As such, the full model was preferred. In this model, there was a significant main effect of age (Wald Chi-Square test: $\chi^2_1 = 4.082$, $p = 0.043$), with individuals being increasingly likely to direct vocalisations towards the face of a social partner with increasing age ($\beta = 0.148$, $SE = 0.073$, $Z = 2.020$, $p = 0.043$). A direct comparison of the age effect (or lack of) between the gaze and face directedness models is shown in Figure 2b. There was also a significant main effect of call type (Wald Chi-Square test: $\chi^2_3 = 17.708$, $p < 0.001$), with vocalisations being significantly more likely to be directed towards the face of a social partner if they were whimpering ($\beta = 0.797$, $SE = 0.274$, $Z = 2.915$, $p = 0.018$) or screaming ($\beta = 1.166$, $SE = 0.453$, $Z = 2.577$, $p = 0.049$) compared to grunting. However, a significant interaction was also observed between age and call type (Wald Chi-Square test:

$\chi^2_3 = 8.445$, $p = 0.037$) with laughs becoming increasingly likely to be directed towards the face of a social partner with age relative to whimpers ($\beta = 0.381$, $SE = 0.133$, $Z = 2.861$, $p = 0.022$) (Figure 2c). All model values for the preferred model are shown in supplementary results C Table S7.

3.3 | Engagement

A full model that predicted mutual face directedness during vocalisation using an interaction between age and call type was significantly different to a null model (LRT: $\chi^2_7 = 24.326$, $p < 0.001$, $R^2_c = 0.276$). The full model was also significantly different from a reduced model that included age and call type as fixed effects with no interaction between them (LRT: $\chi^2_3 = 12.84$, $p < 0.001$). The full model was therefore preferred. In the full model, there was no significant main effect of age. However, there was a significant main effect of call type (Wald Chi-Square test: $\chi^2_3 = 18.823$, $p < 0.001$), with mutual face directedness being significantly more likely to occur if the vocalisation was a scream compared to a laugh ($\beta = 1.779$, $SE = 0.593$, $Z = 3.002$, $p = 0.014$), or a grunt ($\beta = 1.710$, $SE = 0.513$, $Z = 3.335$, $p = 0.004$). There was, however, also a significant interaction between age and call type (Wald Chi-Square test: $\chi^2_3 = 11.729$, $p = 0.008$) with screams being significantly less likely to occur dur-

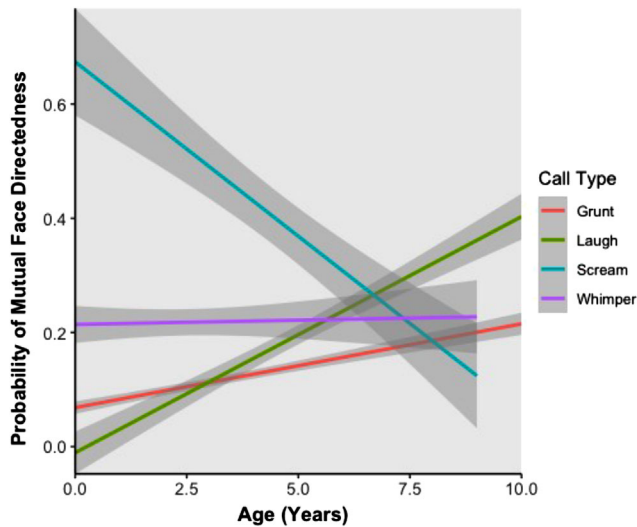


FIGURE 3 Main effects and interactions of the preferred engagement model. Grey areas indicate 95% confidence intervals.

ing mutual face directedness as age increased relative to laughs ($\beta = 0.629$, $SE = 0.200$, $Z = 3.145$, $p = 0.009$) (Figure 3). All model values for the preferred model are shown in supplementary results D Table S8.

4 | FUNCTION OF DIRECTEDNESS AND ENGAGEMENT DURING VOCAL COMMUNICATION

4.1 | Directedness

A model using gaze directedness to predict whether or not a social partner would change their behaviour in response to a vocalisation was not significantly different from a null model (LRT: $\chi^2_1 = 0.405$, $p = 0.524$, $R^2_c = 0.363$), suggesting gaze directedness does not modify the chances that a vocalisation will elicit a behavioural response from a social partner. However, a model using face directedness to predict whether or not a social partner would change their behaviour in response to a vocalisation was significantly different from a null model (LRT: $\chi^2_1 = 4.209$, $p = 0.040$, $R^2_c = 0.335$) (Figure 4), suggesting that if a vocalisation is directed towards the face of a social partner, it is more likely to elicit behavioural change ($\beta = 0.553$, $SE = 0.267$, $Z = 2.068$, $p = 0.038$). All raw values are shown in supplementary results A Table S5.

4.2 | Engagement

Similar to gaze directedness, a model using mutual face directedness to predict whether or not a social partner would change their behaviour in response to a vocalisation was not significantly different from a null model (LRT: $\chi^2_1 = 1.182$, $p = 0.276$, $R^2_c = 0.343$).

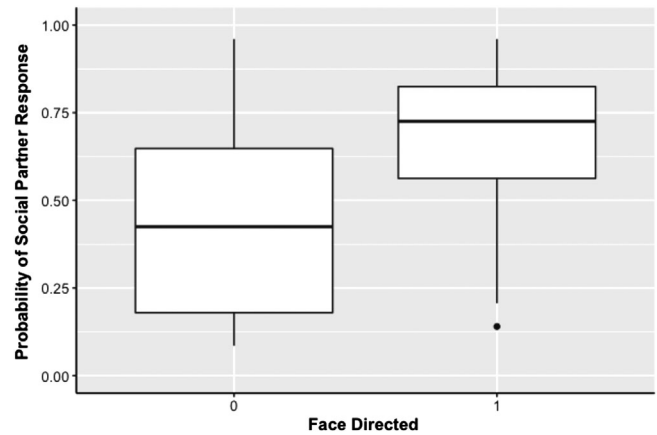


FIGURE 4 Main effects of models that successfully predicted social partner responses with face directedness (0 = not face directed, 1 = face directed).

5 | DISCUSSION

This study aimed to assess the ontogeny of directed vocal communication and engagement during vocal communication in chimpanzees and evaluate its impact on social interactions. We found that young chimpanzees routinely show signs of directedness and engagement during vocal communication. Face directedness showed a general increase during ontogeny. Interestingly, face directedness increased the chances of a call eliciting a behavioural response from a social partner. All other ontogenetic changes in directedness and engagement during vocal communication depended on the call type.

Much like human infants, chimpanzees routinely directed their vocalisations and visually engaged with others during vocal communication from a young age. Fifty-six percent of vocalisations were directed towards a conspecific using gaze, 34% of vocalisations were directed towards the face of a conspecific, and mutual face directedness occurred during 17% of vocalisations. Interestingly, studies of human infant protophones also show approximately 30%–40% of vocalisations were directed towards a social partner (Long et al., 2020). Although, it is important to acknowledge that most human infant data (e.g., Long et al., 2020; Oller et al., 2013) was collected during laboratory conditions wherein caregivers are often instructed to interact with their infants whereas this cannot be controlled in primatological studies. Furthermore, despite the apparent similarities between human infants and young chimpanzees, rates of vocal production in chimpanzees were comparatively low. In fact, the young chimpanzees of this study vocalised on average 0.06 times per minute, approximately 75 times lower than the 4.5 times per minute observed in human infants (Oller et al., 2019). This is also considerably lower than vocal rates in bonobos, who vocalise approximately 18 times less than human infants at 0.24 times per minute (Oller et al., 2019). Further research is needed to convincingly demonstrate these apparent species differences, since current volubility estimates for each species are extracted from studies conducted with the aim of testing different hypotheses and are therefore not methodologically comparable. Nonetheless, the



currently available data on chimpanzees do support the argument that was previously made, on infant great apes vocalizing notably less than infant humans (Oller et al., 2019).

Gaze directedness, face directedness, and mutual face directedness during grunts and whimpers were all observed within the first month of life, with directedness and mutual face directedness for all other call types being observable within the first 2 years (see supplementary results A for raw values). This observation contrasts somewhat with Laporte and Zuberbühler's (2011) study of wild chimpanzee grunts during the first 15 years of life, wherein it was reported that vocal communication during mutual face directedness did not occur, but they observed 'directed' vocalisations from 2 months of age onwards. Consistent with our findings, previous (non-vocalisation) research on chimpanzee infants within the first 3 months of life has shown that chimpanzees show mutual gaze within the first month, but population differences emerged later from 2 months onwards, which appeared to be related to differences in the amount of tactile social interaction (Bard et al., 2005). This suggests inconsistencies across studies may represent legitimate differences (rather than non-replications). This also raises the important point that engagement across human cultures is not universally visual and often tactile instead (e.g., Negayama et al., 2015), indicating that while engagement may be important for language development, *visual* engagement per se may not be essential. Further primate studies could also explore the impact of such forms of engagement on communicative development.

Face directed vocal behaviour did increase generally (i.e., independent of call type) during ontogeny and also was followed by an increased probability of eliciting behavioural responses in a social partner. This is distinct from the apparent lack of an age effect for gaze directedness as shown by a direct comparison of the age effect for gaze and face directedness in Figure 2c. Nonetheless, this provides evidence that the use of directed cues is a social competency that improves in ontogeny and is important for effective communication, as is observed in human vocal ontogeny (see Donnellan et al., 2020). Gaze directedness does not require the subject to be within the line of sight of a recipient (i.e., the subject could be behind a recipient and gaze at them while vocalising), whereas face directed communication is much more likely to be within the line of sight of a recipient. This may help to explain why calls with gaze directedness were not more likely to elicit behavioural responses – often recipients may not know they are the target. However, several important questions remain. Firstly, it is unclear why face directedness during vocal production elicits behavioural responses in social partners. One explanation is that face directedness may provide additional information for the interpretation of vocalisations through concurrent facial behaviours, which can indicate an individual's affective state in chimpanzees (Parr et al., 2007), thereby enhancing a social partners' ability to understand the subjects' communicative act and in turn respond to it. Alternatively, since face directed gaze increases arousal levels in humans (Hietanen et al., 2008; Pönkänen et al., 2011), the increased chances of eliciting behavioural change in a social partner could be arousal-mediated. Relatedly, social partners may be in closer social proximity to subjects during face directed vocal communication, making them more likely to

respond to calls. Although, for all types of directedness studied here, calls were only coded as directed if there was a social partner, meaning both subject and social partner were engaged in social interaction whether the call was gaze directed, face direct, or produced during mutual face directedness. Consequently, the subject and social partner were usually in close proximity in all cases of directed vocalisation. Secondly, it is not clear why face directedness during vocal production increased throughout chimpanzee ontogeny. In human infants, those who have mothers that are more responsive to vocal communication show more directed vocal behaviour later in ontogeny (Gros-Louis et al., 2014), which in turn influences language development (Donnellan et al., 2020). Although, these studies were conducted mainly with western samples wherein face directed communication is more common, whereas in other cultures face-to-face communication is more infrequent (e.g., Fogel et al., 1988). Thus, the extent to which such patterns are typically human remains somewhat unclear. We were not able to assess these possibilities in the present study because they require a longitudinal design (see D'Odorico et al., 1997) and data from multiple populations. While time-consuming, such datasets can be certainly acquired with more systematic monitoring of mother-infant dyads throughout time and across populations.

Face directedness, but not gaze directedness, showed an interaction between age and call type, with laughs becoming significantly more face directed with age relative to whimpers. Thus, while the use of directed cues for whimpers was present from early in ontogeny, the use of directed cues was a competency that emerged in ontogeny for laughs in particular. Similar patterns have also been observed in human infants, wherein laughs were directed towards social partners 78% of the time (compared to 43%–46% for protophones and cries, see Oller et al., 2013 supplementary results), suggesting a similar function for directed vocalisations in both human and chimpanzee vocal communication perhaps relating to social bonding. In chimpanzees, studies of laughter during chimpanzee play show that laughter provides positive feedback to social partners to continue behaviours that might otherwise escalate into aggression (Matsusaka, 2004). Older chimpanzees are also known to be more likely to exhibit aggressive behaviour than younger individuals (Anestis, 2006). Since directed forms of communication can reduce ambiguity in communication (Scott-Phillips, 2015), the use of directed cues during laughter may reduce ambiguity during playful interactions, which becomes increasingly important with age. Additionally, laughter in apes and humans is largely related to the formation and maintenance of social bonds (Bryant et al., 2016; Davila-Ross et al., 2011), suggesting directedness could play an important role in this process, particularly later in ontogeny when individuals have a more diverse set of bonds in their social network (Goodall, 1990).

Both face and gaze directedness did show a similar effect of call type, mostly occurring during whimpers and screams. This contrasts what has been observed in the human infant literature. Human infants do not direct negatively valenced calls such as cries and screams to specific social partners using gaze as often as other vocal types such as laughs (see Oller et al., 2013 supplementary materials). However, screams and whimpers are strong indicators of negative affect in young chimpanzees (Dezecache et al., 2020; Taylor, 2020). For whimpers,



which are mostly used during mother-offspring interactions (Plooi, 1984), this may reflect species differences in parenting behaviours between humans and chimpanzees. Humans typically practice alloparental care more so than chimpanzees, meaning it may be more important for young chimpanzees to identify a specific call recipient to elicit beneficial responses because care is mainly provided by specific individuals. Screams are usually used during agonistic interactions (Goodall, 1990). Third-party intervention in agonistic interactions is dependent on the characteristics of those involved (e.g., Romero & de Waal, 2011). Directing gaze towards another individual during screaming may provide information to others about who has been involved in a conflict. Furthermore, given evidence of acoustically distinct scream types depending on an individual's role in an agonistic interaction (i.e., victim or aggressor: Slocombe & Zuberbühler, 2005) directed screaming may also provide information about who played what role in an agonistic interaction, thereby influencing when third-party responses occur.

The lack of an age effect on mutual face directedness during communication is consistent with previous studies that reported mutual gaze occurred between mother-offspring dyads from early in chimpanzee ontogeny (Bard, 1994; Bard et al., 2005). Mutual face directedness was significantly more likely to occur during screams, but mutual face directedness during screams also seemed to reduce with age. That mutual face directedness mostly occurred during screams contrasts the view that mutual gaze is typically associated with affiliative interactions (e.g., Feldman, 2012) and the expression of positive affect in infants (Colonnesi et al., 2012). However, mutual gaze primarily indicates engagement (Reddy, 2010), and while engagement might often occur during affiliative interactions, there is no reason to expect it is limited to them. Engagement provides a means by which individuals can understand others' psychological states (Reddy, 2010, 2019). For chimpanzees, this might be particularly important in the agonistic interactions during which screams typically occur and wherein the risk of incurring physical injury and damaging social bonds is high (Goodall, 1990). However, since aggression is more common in older individuals (Anestis, 2006), this begs the question of why mutual face directedness during screams significantly decreases during ontogeny. Screams are associated not only with agonistic interactions but also excitement (Clark, 1993; Clark & Wrangham, 1993; Goodall, 1990) and are known to be used in combination with other call types. For instance, scream-like calls are incorporated into chimpanzee pant-hoots (Crockford & Boesch, 2005), which generally occur outside of dyadic social interactions and are largely produced by older males (Fedurek et al., 2013). In a recent study, we also showed that screams are more flexibly produced across affective states in older individuals (Taylor, 2020). As such, the observed decrease in mutual face directedness during screams in ontogeny may be related to an increase in the use of screams outside of the context of dyadic aggression.

Before concluding, it is important to note the possible influence of factors other than communicative competency and effort on the observed patterns of directedness and engagement in the present study. For example, face directedness is likely closely tied to social proximity. Therefore, calls produced during close social proximity, such

as laughs which typically occur during dyadic play (Davila-Ross et al., 2011), may be more likely to show signs of directedness. Although, we in fact observed that whimpers, which are commonly produced during social separation (Dezecache et al., 2020), showed higher levels of directedness than other call types, suggesting our observations of directedness do indeed indicate some degree of communicative competency. An additional influence that appears relevant to directedness is the orienting responses of social partners to calls. For example, if an infant produces a whimper which leads a mother to orient towards the infant, this call may be more likely to be coded as directed. In human infant studies, such influences can be more easily controlled by observing infants in a laboratory (e.g., Oller et al., 2013). However, these factors cannot be controlled among chimpanzees in semi-naturalistic settings. This dissimilarity is likely exacerbated by locomotor differences between the present sample which comprised chimpanzees up to 10 years of age and previous human infant studies which generally focus on individuals within the first 2 years of life (e.g., Donnellan et al., 2020; Gros-Louis et al., 2014). Consequently, differences in the social and physical environment in which observations occurred between the subjects of this study and those of related studies on human infants may in part explain apparent differences in patterns of directedness. In future studies, it will be beneficial to examine the fine-grained patterns of social interaction surrounding vocal communication to improve our understanding of the role of directedness, perhaps utilising conversation-analytic techniques that have recently been successfully used to provide new insights into the ontogeny of gestural communication in chimpanzees and bonobo dyads (Fröhlich et al., 2016) and improve direct comparability with human research where such techniques have also been commonly used (Fröhlich, 2017).

To conclude, in the present study we aimed to examine the ontogeny of directedness and engagement during chimpanzee vocal communication. We found that much like human infants, young chimpanzees routinely show directedness and engagement during vocal communication. Directedness appears to be a social competency that improves during ontogeny and enhances the effectiveness of vocalisations. Unlike human infants, however, directedness and engagement were mostly associated with calls that express negative affect such as whimpers and screams. Our findings therefore highlight both similarities and differences with patterns of directedness and engagement that are observed in human vocal ontogeny. However, since directedness and engagement are considered to be important turning points on the path towards language acquisition in human infants (e.g., Donnellan et al., 2020), the present observations suggest that they may have offered a route towards language phylogenetically, as well as ontogenetically.

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CONFLICT OF INTEREST

The authors have no conflicts of interest to disclose.

DATA AVAILABILITY STATEMENT

All data will be made freely available upon request. All data and scripts used for data analyses are freely available as supplementary materials.

ETHICS STATEMENT

This research was ethically approved by the University of Portsmouth Animal Welfare and Ethical Review Body (AWERB) and Chimfunshi Research Advisory Board (CRAB). We have not reproduced any materials from other sources.

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