Sensitivity to the communicative partner's attentional state: a developmental study on mother-infant dyads in wild chimpanzees (*Pan troglodytes schweinfurthii*)

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Abstract

Gestural communication permeates all domains of chimpanzees' social life and is intentional in use. However, we still have only limited information on how young apes develop the socio-cognitive skills needed for intentional communication. In this cross-sectional study, we document the development of behavioural adjustment to the recipient's visual attention – considered a hallmark of intentional communication – in wild immature chimpanzees' gestural communication. We studied 11 immature chimpanzees (*Pan troglodytes schweinfurthii*): 3 infants, 4 juveniles, and 4 adolescents gesturing towards their mother. We quantified silent-visual, audible, and contact gestures indexed to maternal visual attention and inattention. We investigated *unimodal adjustment,* defined by the capacity of young chimpanzees to deploy *fewer* silent-visual signals when their mothers did not show full visual attention towards them as compared to when they did. We then examined *cross-modal adjustment,* defined as the capacity of chimpanzees to deploy *more* audible-or-contact gestures gestures than silent-visual gestures in the condition where their mothers did not show full visual attention as compared to when they did. Our results show a gradual decline in the use of silent-visual gestures when the mother is not visually attentive with increasing age. The absence of silent-visual gesture production toward a visually inattentive recipient (complete *unimodal* adjustment) was not fully in place until adolescence. Immature chimpanzees used more audible-or-contact gestures than silent-visual ones when their mothers did not show visual attention and vice-versa when they did. This *cross-modal* adjustment was expressed in juveniles and adolescents but not in infants. Overall, this study shows that infant chimpanzees were limited in their sensitivity to maternal attention when gesturing, whereas adolescent chimpanzees adjusted their communication appropriately. Juveniles

present an intermediate pattern with cross-modal adjustment preceding unimodal adjustment and with variability in the age of onset.

Keywords: Intentional communication, visual attention, chimpanzees, mother-infant dyads, development

i. Introduction.

Gestural communication permeates all aspects of great apes' social lives from infancy to old age, and from soliciting nursing or grooming, to soliciting sex or reconciliation. Great apes employ their gestures in communication that is directed to a particular partner (Genty et al., 2009; Leavens et al., 2004a; Liebal et al., 2006; Pika et al., 2003, 2005; Tomasello et al., 1989), and show sensitivity to their partner's visual attention by shifting the modality of their gestural signals to match the channels of information that their partner is able to perceive (Genty et al., 2009; Hobaiter & Byrne, 2011a; Liebal et al., 2004, 2005; Tomasello et al., 2007). This communicative adjustment to the recipient's state of visual attention (their ability to receive the visual information in the signal) is a key feature of intentional communication, and one of the criteria used to infer that a signal is intentionally produced (that is directed to a particular partner in order to achieve a particular goal that the signaller has in mind; Fröhlich et al., 2018; Leavens et al., 2004a).

In order to adjust communication to a partner, apes must be capable of discriminating subtle cues of attention in others (Hostetter et al. 2007; Tempelmann & Kaminski, 2011) or even, for some authors, assigning them a mental state (i.e., here attentional state; Dennett, 1983). Human children show a transition from perlocutionary (broadcast) to illocutionary (targeted and intentional) communication over the first year of life (Bates et al., 1975). A perlocutionary act creates an effect on the audience (e.g. a parent's response to the hunger cry of a newborn infant), whereas an illocutionary act is a conventional social act, recognized by both signaller and recipient that necessarily implies intentional communication on the part of the signaller (e.g. indicating an object with a pointing gesture; Bates et al., 1975). Longitudinal studies of great ape infant communication remain rare, and we still have only limited information on how young apes develop the socio-cognitive skills needed to recognise other individuals' behaviour and/or minds, in order to produce intentional gestural communication.

The shared intentional nature of both great ape gestural communication and human language has been used to argue that gestures may have represented a precursor state in human language evolution (Arbib et al., 2008; Armstrong & Wilcox, 2007; Corballis, 2002; Hewes, 1992; Tomasello, 2008). Given the importance of intentionality for this argument, there has been substantial focus on establishing its presence, and different research groups provide particular behavioural criteria to define intentional signals (Leavens et al., 2005; Townsend et al., 2017). Three main hallmarks are regularly employed: *audience checking*, *persistence to the goal*, and *sensitivity to the recipient's attentional state* (Leavens et al., 2005; Townsend et al., 2017). While these stem from the research describing the transition to illocutionary communication in human infants (Bates et al., 1975), research on great ape gesture has largely focused on using associated criteria to detect intentional communication in juvenile and mature individuals where it is already clearly present (Cartmill & Byrne, 2007, 2010; Christiansen & Kirby, 2003; Hobaiter & Byrne, 2011a; Leavens et al., 2005; Liebal et al., 2004).

Sensitivity to the recipient's attentional state is operationalized in terms of communication match/mismatch between the sensory modality of the signal and the modalities that can be perceived by the recipient. Signals *match* recipient's attention when they are conveyed in a modality that can be perceived by the recipient. Communication *mismatch* occurs when the signaler addresses a visually inattentive recipient with a silent-visual signal (waving when your recipient has turned away from you), or an auditorily inattentive recipient with an audible signal (talking across a noisy bar). Individuals display attention-sensitive signaling when communication mismatches are absent or in a significant lower proportion than communication matches. Two descriptors of communication match/mismatch can be used to address attention-sensitive signaling. *Unimodal adjutment* refers to the capacity of the signaler to deploy *fewer* signals of a given modality '*x*' when they are unable to be perceived, as compared to when they are able to be percieved, i.e., avoiding communication mismatch. *Cross-modal adjustment* refers to the capacity of the signaler to not only inhibit the production of signals of modality '*x'* that cannot be perceived by the recipient, but also to deploy more signals that include other modalities (i.e. '*y'* and/or *'z')* that can be perceived, rather than signals of modality *'x',* as compared to the condition in which signals of modality '*x'* can be perceived, i.e., switching across modalities to favor communication match.

Many gestures incorporate multiple sensory modalities – all gestures include a visible component, but some also include physical contact or audible sound (Hobaiter & Byrne, 2011a; Pika et al., 2003; Tomasello et al., 1994, 1997). Visual attention is relatively easy to infer, for example via gaze and head direction (Hostetter et al., 2001, 2007; Kaminski et al., 2004; Leavens et al., 2004a,2004b; Leavens et al., 2010; Povinelli et al., 2003; Tempelmann et al., 2011); however, it is much more difficult for a human observer to detect another individual's attention towards audible or tactile signals, as it does not require the recipient to display an observable position. For example: many primates, including humans, tilt their head and orient an ear to a sound they are attending to, but we are not incapable of receiving signals in the auditory modality from other positions. While primate recipients have physical limitations on the auditory or contact information they can detect (for example sounds above or below a particular frequency), these are relatively stable – and do not vary substantially with the particular orientation and environment of the signaler-recipient pair. It is possible that a recipient who is paying attention to one set of sounds may be inhibited (or primed) in its ability to perceive another, or that pre-existing physical contact with a signaller alerts the recipient to the possibility of further information in that modality. For example, the physical contact between the mother and her offspring could be defined as a specific form of parental engagement involving physical attention from both mother and infant (Falk, 2004; Mehr & Krasnow, 2017). But, neither case provides observers with a consistent externally observable indication of these states of attention. As a result, studies exploring the sensitivity of a signaller's to their audiences attention have focused on visual-silent gesture use (Fröhlich et al., 2018; Hobaiter & Byrne, 2011a; Hostetter et al., 2007a; Kaminski et al., 2004; Leavens et al., 2004a, 2010; Liebal et al., 2004; Tempelmann & Kaminski, 2011; Tomasello, 2008).

One early hypothesised function for gestures that include audible and contact components was that they served only to regain the recipient's visual attention in cases of visual inattention (*manipulation* by means of *attention-getters*; Tomasello et al., 1994). If this were the case, these gestures should typically be followed by an additional visual signal, should not be used individually, and should only be used when visual attention was unavailable. However, studies of great apes gesturing across age groups found little evidence for attentional *manipulation* (as sequences of audible/contact + silent-visible gesturing; *Gorilla gorilla:* Genty et al., 2009; *Pan troglodytes:* Hobaiter

& Byrne, 2011b; Liebal et al., 2004). Instead, where visual attention was not present, signallers of any age either moved to place themselves in the line of sight (*unimodal adjustment*; *Pan troglodytes, Pan paniscus:* Liebal et al., 2004b), and/or selected a gesture that conveyed the information in an alternative modality (*cross-modal adjustment*), for example through sound or touch (*Pan troglodytes*, mixed ages: Hobaiter & Byrne, 2011a; *Pan paniscus*, infants and juveniles: Pika et al., 2005); suggesting that gestures of all modalities convey information, including in non-visual channels.

Further evidence for chimpanzees' ability to adjust their signal use comes from captive studies employing *food-requesting* paradigms. Here, captive chimpanzees (*Pan troglodytes*) need to communicate with a human experimenter to access food. Chimpanzees were capable of *unimodal adjustment* of silent-visual signals: producing significantly more silent or silent-gesture+vocal communication when human experimenters were visually attentive than when they were not (*Pan troglodytes*: (adults and adolescents) Hostetter et al., 2001, (mixed ages) 2007b; (mixed ages) Kaminski et al., 2004; (adults) Leavens et al., 2004b, (adults) 2010; (5-year old chimpanzees) Povinelli et al., 1996; *Pongo pygmaeus, Gorilla gorilla, Pan paniscus, Pan troglodytes* (mixed ages): Tempelmann et al., 2011). Nevertheless, like studies of their conspecific communication, the majority of these experiments focused on the behaviour of mature great apes, leaving open questions on when and how modal adjustment in chimpanzee communication emerges.

Only a few studies have examined sensitivity to the recipient's visual attention in immature apes (e.g. Fröhlich et al., 2019; Tomasello et al., 1997). In a young chimpanzee's life – the mother is typically a privileged partner, and mother-infant relationships are considered a "developmental niche" that shapes behavioural ontogeny (Stamps, 2003; West et al., 2003). The emergence of the different gestural modalities appears to parallel changes in mother-infant interactions. Contact and silent-visual gestures appear earlier in young chimpanzees (around 8 months of age) than audible gestures (around 18 months of age), and the use of silent-visual gestures increases while that of contact and audible gestures decreases with age (Schneider et al., 2012). In chimpanzees, body contact with the mother gradually decreases across infancy, and is limited by the time weaning occurs at around 5-years of age (Clark, 1977; Nishida, 2012). Over the juvenile period (from 5-years to puberty at ~10 years), proximity to the mother further decreases, with an increasing tendency to move out-of-sight and at times to travel independently. Thus, during their development, young chimpanzees experience progressively increasing physical distances to their mother, potentially promoting the use of distal communication and hence the use of more silent-visual and/or audible gestures (Fröhlich et al., 2016; Lonsdorf et al., 2014).

Here, we document the development of young chimpanzees' gestural communication within the mother-infant dyad from infancy to adolescence. We focus on differences in the modality of immature chimpanzees' gestural signals, given their mother's visual attention. First, we describe immature chimpanzees' use of the different modalities of gesture, and how these are combined into sequences. We then investigate whether immature chimpanzees employ *unimodal adjustment;* producing *fewer* silent-visual signals when their mothers did not show full visual attention towards them as compared to when they did. Second, we investigate whether immature chimpanzees employ *cross-modal adjustment*; producing *more* audible-or-contact gestures than silent-visual gestures where their mothers did not show full visual attention as compared to when they did (Leavens et al., 2004b, 2010; Liebal et al., 2004; Tomasello, 2008). To do so, we test whether they differentially produce silent-visual and audible-or-contact gestures across conditions of maternal visual attention.

ii. Methods.

The research adhered to the legal requirements of the countries in which it was conducted and to the principles of the ‘‘Ethical Treatment of Nonhuman Primates,’’ as outlined by the American Society of Primatologists. All original video data collection occurred with permission from the Ugandan National Council for Science and Technology, the Uganda Wildlife Authority, and the Budongo Conservation Field Station, following ethical review by the University of St Andrews Animal Welfare and Ethics Committee, and followed the International Primatogical Society’s Code of Best Practices for Field Primatology.

Study sites and subjects

Original video data for this study were extracted from the Great Ape Dictionary video database and then further coded (www.greatapedictionary.com). This database contains labelled video-data and a set of coded gestural signals produced by wild apes during communication across species and sites. The data coded for this study were originally collected in the Budongo Forest Reserve in North-West Uganda (Eggeling, 1947) from the Sonso community of East African chimpanzees (*Pan troglodytes schweinfurthii*), and are fully reported in Hobaiter & Byrne (2011a). Original data collection started in October 2007. At this time, the community consisted of 81 named individuals including 18 infants (3 males and 15 females) aged between 0 and 4 years old, 15 juveniles (6 males and 9 females) aged between 5 and 9 years old, and 16 adolescents (10 males and 6 females) aged between 10 and 15 years old (more details: Hobaiter & Byrne, 2011a; Reynolds, 2006).

In this cross-sectional study, we focused on development across three developmental periods: infant (0-54 months), juvenile (55-102 months), and adolescent (103-180 months). The transition from infancy to the juvenile period is marked by the period in which the mother stops breastfeeding and the infant ceases to travel on the mother's body, and typically occurs around 4 or 5 years old in wild chimpanzees (Clark, 1977; Nishida, 2012). The transition from the juvenile period to the adolescence is defined by puberty which typically occurs around the age of 8 or 9 years old in wild chimpanzees (Pusey, 1990) and is marked by the development of secondary sexual characteristics, and full independence from the mother. The transition from the adolescent period to adulthood typically occurs around 15 years old, but is more variable (Nishida, 1988; Pusey, 1990). As detailed longitudinal data on individual behavioural or physiological changes were not available, we used fixed age categories across individuals. We extracted coded gesture data for individuals in each of the three developmental categories who had produced at least 10 gestures in communication with their mother. The final data set selected for this study included 264 gestures produced by 11 individuals (see Table 1): 3 infants (1 male and 2 females; aged between 15 and 53 months), 4 juveniles (2 males and 2 females; aged between 57 and 102 months), and 4 adolescents (1 male and 3 females; aged between 107 and 175 months, see Table 1).

Data collection

Original video data were collected by CH during three field periods between October 2007 and August 2009. For full details of the data collection method, see Hobaiter & Byrne (2011a). Data were collected using a *focal behaviour* sampling approach (Altmann, 1974). Any social interaction with the potential for communication was filmed, in practice all occasions in which two or more individuals were present and not occupied in solitary activities such as resting or self-grooming were considered an opportunity to film. When multiple opportunities to film were available, preference was given to those social contexts in which previous research suggested gestural communication was prolific (for example play) or to individuals for whom available data were more limited. A running record of the frequency with which individuals were observed was maintained in order to target infrequently sampled individuals. However, as East African chimpanzees are highly fission-fusion, with some individuals observed near daily, and others absent for several weeks or months, there remain differences in the frequency with which it was possible to observe particular individuals. As a result, some individuals are better represented, or represented over a longer period in the final dataset. Video data were recorded using a Sony Handycam (DCR-HC-55) and MiniDV tape. Videos were relatively short, typically lasting between 2 and 3 minutes, but a single communicative event often included several gestures towards the mother. 141 video clips were selected for further coding in this study (a mean of 12 recordings per individual).

Behaviour sampling/Coding procedure

Gestures were originally coded following the repertoire used in the original data collection, with interobserver coding conducted on 11% of the original data set by a 2nd coder with expertise in great ape gestural communication (full details in Hobaiter & Byrne, 2011a). To be considered for coding, all gestures must be produced during intentional communication by definition. In practice this meant that any potential cases of gesture must be accompanied by behavioural indications of intentional use (response waiting, audience checking, persistence). Gestures in which there was no clear evidence of intentional use, or where it was not possible to identify a specific recipient (for example more than one potential recipient) were excluded (interobserver reliability coding of Directedness, Cohen's kappa: K=0.69). In the current dataset, only those gestures that were marked as directed and where the recipient was the mother were considered for analysis.

The full repertoire included over 60 gesture types (Byrne et al., 2017; Hobaiter & Byrne, 2011a; interobserver reliability coding of Gesture Type, Cohen's kappa: K=0.86) gesture types were further categorised as a function of their predominant sensorial modality into three groups: auditory, contact, or silent-visual (Byrne et al., 2017). All gestures include a visual component. Gestures that additionally produce a sound as a consequence of the specific gesture action, were defined as *audible* gestures. Gestures that include physical contact as a consequence of the specific gesture action (which may or may not also produce a sound) were defined as *contact* gestures.

In this study, for each gesture, the following information was extracted from the original data: the main sensory modality (audible, silent-visual, or contact), the situational context, if the signal was produced as a single gesture or used in a sequence of gestures, and, if in a sequence, its position relative to other gestures. Given our focus on visual attention in assessing maternal attentional state, at times we considered the use of audible or contact gestures, both suitable for transmitting information to a visually inattentive recipient, as a combined category: audible-or-contact.

As in other studies (e.g. Hobaiter & Byrne, 2011b), we distinguish: *single gestures,* defined by the fact that a gesture is followed by a pause of 1 second or more from *gestures sequences* where 2 or more gestures are produced and separated by less than 1 second. The 1-second interval is taken to be the minimum time required for response-waiting to occur (e.g. Hobaiter & Byrne, 2011b), and so in this case gesture sequences are considered to be single communicative units, rather than reflecting persistence or modification of the communication by the signaller. Persistence would refer to the addition of further single gestures or gesture sequences after a pause of 1-second or more.

For the gesture cases extracted in this study the majority were recorded during social play (34%), feeding (33%), and grooming (23%); but data also included gestures recorded during traveling (5%), affiliation (2%), agonism (<1%), patrolling (<1%), resting (<1%), and unknown (<1%) contexts. To this coding, we added three new variables: maternal-attention, the *within-sequence modality*, and the *modal dimension* (unimodal, bimodal, or trimodal) of the sequence.

Maternal attention was defined by the mother's *visual attention* (original interobserver coding of the original variable, Attentional state: Cohen's kappa: K=0.63). We refined the coding of visual attention in the original data to employ a tighter definition of attention, so that in the current dataset a mother was only marked as 'attending' when she was looking directly at her offspring (marked using head orientation or gaze) immediately prior to the onset of the gesturing by the immature signaller. Mothers who had partial or peripheral view, or no view of their offspring were all marked as not attending. Thus, our attention variable had two conditions: 1) *visual-attentive*: the mother's face is fully oriented towards the infant; if the recipient's direct line of sight is considered to be at 0° the signaller could be located only within an arc 45° either side of this; 2) *visual-inattentive*: the mother's face is not fully oriented towards the infant; the signaller is located at an angle of 45° or greater from the recipient's direct line of sight. Examples of gestures produced by individual in each of the three developmental age categories and for each of the maternal attention conditions are available here: Dafreville et al Sensitivity to the communicative partner's attention state.

We defined sequence modality for all sequences of two or more gestures. Sequence modality was described in two ways. 1) *within-sequence modality* indicated the succession of gesture modalities that composed the sequence [for example a 3-gesture sequence composed of a *hit other – object move – stomp object* was coded as Contact-Audible-Audible (CAA); a 2-gesture sequence composed of *Dangle – Swing* was coded as Audible-Silent (AS)]. 2) *modal dimension,* which describes how many of the three modalities of information (silent-visual, audible, contact) were incorporated into the sequence (unimodal, bimodal, or trimodal).

Statistical analyses

We tested the effect of increasing age on the capacity for *unimodal adjustment* by fitting generalized linear mixed models (GLMM) using a Poisson error distribution and a log link function (Bolker et al.,

2009) using the function *glmer* of the R package *lme4* version 1.1-23 with the optimizer function of *aictab* of the R package *AICcmodavg* to calculate AICc that is a transformation of the Akaike's Information Criterion (AIC) used for small sample. We coded a 'match' (0) when an immature chimpanzee produced a silent-visual gesture to a visually attentive mother, and a 'mismatch' (1) when they produced a silent-visual gesture to a visually inattentive mother. As fixed effects we included age of the signaler at the time of the gesture (in months), and we included sex of the signaler (male, female) as a fixed control factor. Signaler identity was included as a random effect. Interactions between fixed effects and random slopes were not included due to incomplete combination matrices. As an overall test of the predictor (age) on a decreasing unimodal mismatching, we compared the fit of the full model with that of a null model comprising only the fixed control effect (sex) and the random effect (signaler identity).

The sample size was small (11 individuals) and the data did not follow a normal distribution, so we performed nonparametric tests (Siegel & Castellan, 1988) and included a Bonferroni correction in the case of multiple comparisons. To test the capacity for *unimodal adjustment*, we compared the number of silent-visual gestures produced by immature chimpanzees when their mothers were visually attentive to when they were not. Note that visual attention was assessed immediately prior to the onset of gesture production, so after any adjustment of signalling location by the offspring had taken place. Firstly, we calculated a weighted mean age for each individual's data (in each maternal visual condition). To do so we calculated mean age weighted by the number of gesture cases recorded at each age point. For example: Karibu produced 3 gestures at 18-months, 10 at 19-months, 9 at 20-months, 9 at 21-months, 5 at 22-months, 7 at 29-months, and 1 at 49-months. The weighted mean age for her gesturing was (3*18+10*19+9*20+9*21+5*22+7*29+1*49)/44, or 22.16 months. Spearman rank order correlation coefficients were used to test the correlation between the proportion of silent-visual gestures and individual weighted mean age in each maternal visual condition.

In unimodal adjustment, as the silent-visual gestures use in attention and inattention conditions are symmetrical, we only tested the correlation between the proportion of silent-visual gestures and individual mean age when the mother shows visual inattention. We then used Fisher exact probabilities tests for independent samples to test the effect of age category on the distribution of silent-visual gestures by condition. To test the capacity for *cross-modal adjustment*, we compared the proportion of audible-or-contact gestures and silent-visual gestures across conditions of maternal visual attention, and we then specifically compared the use of the two types of audible-or-contact gestures in the case of maternal visual inattention. Spearman rank order correlation coefficients were used to test the correlation between either the proportions of silent-visual or audible-or-contact gestures, and individual weighted mean age for each maternal visual condition. Then we used Fisher exact probabilities tests for matched-samples within each age category to test the capacity to vary the production of audible-or-contact gestures and silent-visual gestures across the levels of maternal visual attention. To test the modal preference for *cross-modal adjustment*, we used Spearman rank order correlation coefficients and Fisher exact probabilities tests to test the effect of age category on the proportions of audible and contact gestures when the mother showed visual inattention.

To represent active adjustment of the different gesture modalities towards the maternal visual attention state, we calculated the percentage deviation in the variation in use of audible-or-contact as compared to silent-visual gestures for each condition of maternal attention and age category (as Hobaiter & Byrne, 2011a). The deviation was calculated by $(\beta/\alpha-1)$ x100 with α = number of audible-or-contact gestures/ total number of gestures used in the age-range subgroup, and β = number of audible-or-contact gestures/ total number of gestures used in the condition and age-range subgroup.

As we measured visual attention immediately prior to the onset of gesturing, the impact of these states of attention should be most profound on the first gesture produced (whether as a single gesture, or the first in a sequence). Restricting our dataset to these cases would have substantially reduced our statistical power; however, whenever possible we provide a matching analysis replicated with this smaller dataset in the supplementary materials, to give an indication of the patterns of gesture use in the case of first or single gestures only (see Table S1, S2 and S3 in *supplementary material*). All tests were conducted using R v3.6.1 software (http://cran.r-project.org) with p-value equal or lower than 0.05 required for significance. All statistical tests were two-tailed.

iii. Results.

Individuals from all three age categories produced (total n=264) gestures, including gesture types in each modality (silent-visual, audible, contact), and across both states of maternal visual attention (with and without full visual-attention; see Table 2 and S4 in *supplementary material*).

How are gestures of different modalities combined within gesture sequences?

Within the 208 communication acts coded, single gestures were more prominent than sequences (single gestures n=164; sequences n=44), which ranged from 2 to 4 gestures in length. Infants produced a much larger proportion of their communications as sequences (total communications n=47; sequences n=21, 45%), than juveniles (total communications n=109; sequences n=16, 15%) or adolescents (total communications n=52; sequences n=7, 13%).

The use of multiple modalities of gesture within a sequence occurred at all age categories, and the use of unimodal or bimodal sequences was similarly distributed across all communications (unimodal n=21, bimodal n=22) and within each age category (infant: unimodal n=9, bimodal n=11; juvenile: unimodal n=8, bimodal n=8; adolescent: unimodal n=4, bimodal n=3). We did not observe any sequence with all three modalities of gesture (trimodal). Gesture sequences that included both audible-or-contact and silent-visual gestures (n=16) were not more likely to start with an audible-or-contact gesture (n=9) than with a silent-visual gesture (n=7; see Table S5 in *Supplementary material*).

Unimodal adjustment: does the use of unimodal matching vary with signaller age?

There was a clear influence of age on a decreasing unimodal mismatching (null model comparison: X^2=11.584, df=1, p<0.001). The production of unimodal mismatching, here the use of silent-visual gestures to a visually inattentive recipient, decreased with increasing age (see Table 3). The same patterns held for the subset of gestures that were produced individually or as the first gesture in a sequence (see Table S1 in *supplementary material*).

We tested the correlation between the use of silent-visual gestures and weighted mean age in each maternal visual condition (see Fig.1). We found that the use of silent-visual gestures correlated negatively with age when their mother shows visual inattention (Spearman rank order correlation coefficient, $r = -0.90$, $p = 0.001$, $N=11$). As silent-visual gestures use in attention and inattention conditions are symmetrical, the correlation is exactly inverse when mother shows visual inattention and p-value is the same. The same patterns held for the subset of gestures that were produced individually or as the first gesture in a sequence (see Table S2 in *supplementary material*).

When we considered age as separate developmental categories (see Fig. S1 in *supplementary material*), infants produced relatively few silent-visual gestures (n= 10 out of 77; Table 2) and when they did so there was no evidence that they adjusted these to their mother's visual attention (mother visually inattentive: n= 7; mother visually attentive: n=3). Juveniles produced a larger number of silent-visual gestures (n=54 of total n=126; Table 2) and were more likely to do so when their mother showed prior visual attention (mother visually attentive: n=31; mother visually inattentive: n= 23). Adolescent chimpanzees did not produce silent-visual gestures (n=21 out of 62, Table 2) when their mother did not show prior visual attention (mother visually inattentive: n= 0; mother visually attentive: n=21). We found no difference in the pattern of use between infant and juvenile chimpanzees (Fisher Test, effect size calculated as the odd ratio of log-likelihoods, $OR = 1$, $p=0.68$, $N=7$), but adolescents differed in their use from both infants (Fisher Test, $OR=1$, $p<0.001$, $N=7$) and juveniles (Fisher Test, $OR=1$, $p<0.001$, $N=8$; see Fig. S1 in *supplementary material*). The same patterns held for the subset of gestures that were produced individually or as the first gesture in a sequence (see Table S2 in *supplementary material*).

Individually, none of the infants showed reduced use of silent-visual gestures when their mother did not show full visual attention; whereas half of the juveniles (2 on 4) and all adolescents did so (see Fig. 2).

Cross-modal adjustment: Does the use of different gestural modalities vary according to maternal visual attention?

We tested the correlation between the use of silent-visual gestures or audible-or-contact gestures and weighted mean age in each maternal visual condition (see Fig.S2). We found that the use of audible-or-contact gestures correlated positively with age when the mother showed visual inattention (Spearman rank order correlation coefficient, $r = 0.69$, $p = 0.033$, $N=11$) while there was no significant correlation when the mother showed visual attention (Spearman rank order correlation coefficient, $r = -0.42$, $p = 0.248$, $N=11$). As the use of silent-visual gestures and audible-or-contact ones were symmetrical, the results of correlation are exactly inverse for silent-visual gestures and p-values are the same within each condition. The same patterns held for the subset of gestures that were produced individually or as the first gesture in a sequence (see Table S2 in *supplementary material*).

As the different modalities are not represented with equal frequency in the overall repertoire of gesture types, or in the subsets of gesture types used by each age category (see Table S4 in *supplementary material*), there may be biases in their use because of the availability of gesture types in an appropriate modality. To address this, we explored variation in use from the overall average gesture use within an age category according to the mother's state of visual attention. We found no evidence for *cross-modal* adjustment of silent-visual or audible-or-contact gesture types in infant chimpanzees (mother visually attentive: audible-or-contact gestures n=25, silent-visual gestures n=3; mother visually inattentive: audible-or-contact gestures n=42, silent-visual gestures n=7; Fisher Test, OR=1, p=1, N=3; see Fig.3). However, both juvenile and adolescent chimpanzees increased their use of silent-visual gestures and decreased their use of audible-or-contact gestures when their mothers were attentive, and vice-versa when they were inattentive prior to gesturing (in juveniles: mother visually attentive: audible-or-contact gestures n=24, silent-visual gestures n=31; mother visually inattentive: audible-or-contact gestures n=48, silent-visual gestures n=23; Fisher Test, OR=1, p=0.043, N=4; in adolescents: mother visually attentive: audible-or-contact gestures n=21, silent-visual gestures n=21; mother visually inattentive: audible-or-contact gestures n=19, silent-visual gestures n=0; Fisher Test, OR=1, p<0.001, N=4). When we replicated these tests on the subset of gestures that were produced individually or as the first gesture in a sequence, the same patterns were found for adolescents, but neither juveniles nor infants showed any evidence of *cross-modal* adjustment (see Table S2 and S3 in *supplementary material*).

How are audible-or-contact gestures used when the mother does not have visual attention?

We tested the correlation between the proportions of audible-or-contact gestures and weighted mean age when mother showed visual inattention. We did not find any significant correlation (Spearman rank order correlation coefficient, r = 0.03, p = 0.883, N=11). The same patterns held for the subset of gestures that were produced individually or as the first gesture in a sequence (see Table S2 in *supplementary material*).

When the mother did not show full visual attention towards their offspring, we found a difference in the relative use of different types of audible-or-contact gestures across the three age categories (infant: audible gestures n=13, contact gestures n=29; juvenile: audible gestures n=17, contact gestures n=31; adolescent: audible gestures n=17, contact gestures n=2; Fisher Test, OR=2, $p<0.001$, N=11; Fig. 4). Both infants and juveniles employed more contact gestures and did so in a similar way (Fisher Test, OR=1, p=1, N=7), whereas adolescents employed more audible gestures, and did so to an extent that differed from both infants (Fisher Test, OR=1, $p<0.001$, N=7) and juveniles (Fisher Test, OR=1, $p<0.001$, N=8; Fig. 4). The same pattern was found when we analysed only the subset of gestures produced either singly or as the first in a sequence (see Table S1 in *supplementary material*).

iv. **Discussion.**

This study investigated the development of the ability of immature wild chimpanzees to adjust their gesturing to the visual attention of a recipient, here their mother's. *Sensitivity to the recipient's attention state* is considered a hallmark of intentional communication and one of the core criteria used to infer that a gesture is produced intentionally (e.g. Fröhlich et al., 2018; Leavens et al., 2005; Pika et al., 2005; Tomasello et al., 1997). We find that as immature chimpanzees aged, they showed a decline in their use of silent-visual gestures when the mother's full visual attention was not available, indicating increasing inhibitory abilities that support *unimodal adjustment*. None of the infants showed adjustment of their silent-visual signals given the attentional state of their mother, while two out of the four juveniles and all the adolescents did so. Immature chimpanzees employed *cross-modal adjustment* from the juvenile period onwards, using more audible-or-contact gestures than silent-visual gestures when their mothers did not show full visual attention prior to gesturing, and vice-versa when they did. All immature chimpanzees produced gestures in sequences comprising one or two modalities, but did not initiate their sequences with a particular modality.

Juvenile and adolescent, but not infant, chimpanzees displayed cross-modal adjustment to their mother's visual attention, favouring audible-or-contact gestures over silent-visual gestures when their mothers were visually inattentive. When considering the subset of gestures produced individually or as the first gesture in a sequence, this pattern of adjustment was only found in adolescents. Taken together, these results suggest that infant chimpanzees gesturing was not sensitive to their mother's full visual attention, that of adolescents was, and juveniles displayed an intermediate pattern (Fig. 5).

We also found that infant and juvenile chimpanzees favoured contact over audible gestures to address a visually inattentive mother, whereas adolescents favoured audible gestures in these situations. These results are consistent with previous studies reporting a preference for tactile communication in younger primates (Schneider et al., 2012; Tomasello et al., 1997), and reflect patterns of increasing physical distance between mothers and their offspring with age (Bard, 2019; Fröhlich et al., 2016; Lonsdorf et al., 2014), which may favour the use of audible over tactile gestures, which requires moving to within arms' reach. Our juvenile chimpanzees again showed an intermediate pattern, displaying the same preference for contact gestures as infants, but using these contact gestures to address their mother specifically when her full visual attention was not available.

Juvenile chimpanzees in the Sonso community regularly employ the widest variety of their gestural repertoire, as compared to younger or older individuals (Hobaiter & Byrne, 2011a), and similar results have been found in other primate species (e.g., *Gorilla gorilla*: Genty et al., 2009; *Papio anubis*: Molesti et al., 2020). Here, too, we found that juveniles employed a greater variety of silent-visual gestures as compared to infants and adolescents (see table S4 in *supplementary materials*). Thus, juveniles expand their use of silent-visual gesture types as they begin to display more sensitivity to their partners' visual attention, suggesting that the juvenile period is critical to exploring the repertoire of communicative gestures available and the appropriate ways of using gestures of different modalities.

Juvenile chimpanzees' use of cross-modal adjustment in their gesturing prior to unimodal adjustment was unexpected. From the perspective of executive functioning, unimodal adjustment relies on inhibitory control over the production of signals when a recipient is unable to perceive them. In contrast, cross-modal adjustment relies on flexibility in the deployment of signals across various sensory modalities. Inhibitory control is amongst the earliest executive functions to emerge in human infants, while cognitive flexibility develops more slowly (Anderson, 2002). Following this framework, we would expect to observe unimodal adjustment preceding cross-modal adjustment (at least in human infants); however, empirical support for this developmental trajectory in humans (*Homo sapiens sapiens*) is also mixed. Liszkowski et al. (2008) showed that infants at 12 months old decreased their pointing gestures towards inattentive adults as compared to attentive adults, thereby showing unimodal adjustment. The onset of cross-modal adjustment has been reported prior to this age (~10 months; Wu & Gros-Louis, 2017), at the same age (~12 months; Igualada et al., 2015), and after this age (at ~18 months; Liszkowski et al., 2008). To our knowledge, there is no other developmental study directly comparing unimodal and cross-modal adjustment in non-human primates. However, the broader capacity to show *sensitivity to the recipient's attention state* has been investigated across diverse primates species, both in conspecific interactions and in interaction with human experimenters (e.g., captive population with an experimental design: *Pongo pygmaeus*, *Gorilla gorilla*: (adults) Botting & Bastian, 2019; (adults and adolescents) Poss et al., 2006; *Papio anubis*, mixed ages from 6 to 16 years old: Bourjade et al., 2014; *Macaca tonkeana,* mixed ages from 5 to 13 years old: Canteloup et al., 2015; *Cercocebus torquatus torquatus,* mixed ages from 2 to 23 years old: Maille et al., 2012; wild population with an observational method : *Macaca radiate*, mixed ages: Deshpande et al., 2018); but also across non-primates species in interaction with conspecifics (e.g., *Canis familiaris*, alduts and puppies: Horowitz, 2009; *Corvus corax*, ages from 1 to 2 years old: Pika & Bugnyar, 2011; several coral reef fishes species, mixed ages: Vail et al., 2013) and in interaction with humans (e.g., *Gymnorhina tibicen*, mixed ages: Kaplan, 2011; *Equus caballus*, mixed ages: Proops & McComb, 2010; *Canis familiaris*, adults: Horowitz, 2009; Kaminski et al., 2012; Savalli et al., 2014; Topál et al., 2014) . All these studies tested and found evidence for unimodal adjustment to the recipient's visual attention state but only a few tested and reported cross-modal adjustment (*Papio anubis,* mixed ages from 6 to 16 years old: Bourjade et al., 2014; *Canis familiaris*, adults and puppies: Horowitz, 2009) . All these studies tested and found evidence for unimodal adjustment to the recipient's visual attention state but only a few tested and reported cross-modal adjustment (*Papio anubis,* mixed ages from 6 to 16 years old: Bourjade et al., 2014; *Canis familiaris*, adults and puppies: Horowitz, 2009). Moreover, studies on executive function in baboons (*Papio papio*) have shown that subadults outperformed adults in cognitive flexibility (Bonté et al., 2014), whereas the opposite pattern was found for inhibitory control (Fagot et al., 2008). Further investigation of a non-human primate-typical developmental pattern of executive control and flexibility is required to advance our understanding of the cognitive underpinnings of unimodal and cross-modal adjustment in chimpanzees.

In the present study, juveniles as a group demonstrated both aspects of sensitivity to attention but individual patterns differed sharply for unimodal adjustment, with Night and Zak (one of the youngest and one of the oldest) showing a clear adjustment of their silent-visual gestures to their mother's visual attention, while Karo and Kasigwa did not. Interestingly, Night and Zak also displayed a sharper cross-modal adjustment than the two others (see Figure S3 in *Supplementary material*) again suggesting that cross-modal adjustment may be a developmental precursor to unimodal adjustment in chimpanzees. Fröhlich et al. (2018) found no improvement in sensitivity to the recipient's attention when comparing infant and juvenile chimpanzees. However, each individual showed progression in adjusting its signal modality to the recipient's attention (i.e., within-age effect, see Fröhlich et al., 2018). Although the present sample was insufficient to perform a within-age study and required that we parse continuous development into artificially discreet age-categories, our results still suggest that attention-sensitive signalling may develop at a different pace across individuals.

One potential explanation of the relatively late expression of adjustment capacities in our data is that our definition of maternal visual attention was very restrictive. In our study, maternal visual attention was limited to where the mother had *full view* of the infant and excluded cases where the mother had *partial* or *peripheral view* (as well as those where she had no view at all). However, chimpanzee mothers likely continue to monitor their younger offspring in their peripheral vision (so called 'eyes in the back of their head'). Maternal visual attention may also be difficult to consistently detect; Kano and Tomonaga (2011) showed that chimpanzee eye saccades are shorter and more frequent than humans' and permit faster scans of the environment. If chimpanzee mothers reliably monitor their infants with peripheral vision and respond appropriately to their infants' gestures in these conditions, younger chimpanzees would experience relatively little learning pressure to discriminate subtle differences between full and peripheral attention, and may take longer to fully develop this sensitivity. Once proximity to their mother increases as juveniles and then adolescents, both the mother's ability and need to visually monitor their offspring closely may decline, increasing the pressure on their offspring to refine modal adjustments in their signalling. Interestingly, this may also provide an explanation for why infants were found to prefer 'attending' to non-maternal, rather than maternal, partners (Fröhlich et al., 2018) – if 'mum is always watching' then the early onset of unimodal or cross-modal adjustment may be more easily detected in gesturing towards non-maternal partners. Similarly, differences in maternal attentiveness or mothering 'style' (Stanton et al., 2015) may contribute to individual variation in the onset of modal adjustments in gesturing.

Another possible explanation for the weak effect of maternal visual attention on the gesturing of infant and juvenile chimpanzees in our data may be that the majority of these gestures were recorded in the context of either social play (34%) or feeding (33%). In play, individuals may receive less pressure towards the efficient expression of their communication (Heesen et al., 2019). Fröhlich et al. (2018) examined the effect of communicative context on behavioural markers of intentional communication and while they found no difference between gesturing during play, travelling, and feeding on the sensitivity to recipient attention, they did find an effect on the occurrence of audience checking and persistence.

Conclusion and perspectives

This cross-sectional study on the development of the sensitivity to others' visual attention in chimpanzee gestural communication shows that immature chimpanzees may take several years to refine these skills. Infant chimpanzee did not display either unimodal or cross-modal adjustment and there was substantial variability in the age of onset, with only some juveniles and, finally, all adolescents showing appropriate adjustments. It remains unclear to what extent these findings reflect an inability to do so in infancy, or an absence of the need to do so, given mothers' tendency to monitor young infants closely. Our data suggest that cross-modal adjustment may be a developmental precursor of unimodal adjustment. Future studies should explore how the onset and expression of these abilities are impacted by the identity and behaviour of social partners as well as the individual characteristics of the signaller.

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TABLE 1. Observation age range, weighted mean age, sex, and relationship of the mother–offspring dyads. We show the age, sex, and mother-offspring dyads for all pairs included in the study, together with the number of gestures directed to the mother by the immature chimpanzees. Weighted mean age refers to the mean age weighted by the number of gestures at a given age (see methods).

Age category	Signaller (# gestures)	Mother	Sex	Observation age range (weighted mean age) *(in months)*
Infant	Karibu (44)	Kwera	Female	18- 49 (22.16)
	Klauce (16)	Kalema	Male	15-53 (29.13)

	Kox (17)	Kewaya	Female	15-25 (18.47)
Juvenile	Karo (21)	Kwera	Female	83-102 (93.19)
	Kasigwa (14)	Kutu	Male	60-64 (62.57)
	Night (53)	Nambi	Female	57-77 (63.21)
	Zak (38)	Zimba	Male	68-80 (77.63)
Adolescent	Kumi (11)	Kalema	Female	107-127 (115.73)
	Kwezi (13)	Kwera	Male	129-132 (166.92)
	Nora (19)	Nambi	Female	141-152 (145.68)
	Rose (18)	Ruhara	Female	154-175 (131.11)

TABLE 2. Gesture cases given visual attention of the mother. Number of gestures produced by infant, juvenile, and adolescent chimpanzees in each modality, according to the visual attention of the mother immediately prior to gesture production.

Age category	Gestural channel	Visual attentive	Visual inattentive
Infant (N=3)	Audible	17	13
	Contact	8	29
	Silent-visual	3	7
	Total	***28***	***49***
Juvenile (N=4)	Audible	13	17
	Contact	11	31
	Silent-visual	31	23
	Total	***55***	***71***
Adolescent (N=4)	Audible	17	17
	Contact	4	2
	Silent-visual	21	0
	Total	***42***	***19***
Combined categories (N=11)	Audible	47	47
	Contact	23	62
	Silent-visual	55	30
	Total	***125***	***139***

TABLE 3. Parameter estimates for the tested model – GLMM with the number of silent-visual gestures (n=85) mismatching maternal visual attention as dependent variable and age (in months) as fixed effect. There was a clear influence of age on unimodal matching (null model comparison: X^2=11.584, df=1, p<0.001).

Parameter	Unimodal matching ~ Age					
	Estimate	**SE**	**Lower CI**	**Upper CI**	**Z-value**	**P-value**

(Intercept)	1,029	0,379	0.286	1.773	(1)	(1)
Age(2)	-0,018	0,005	-0.029	-0.008	-3.428	p<0.001

(1) Not indicated because of limited interpretive value

(2) Age: refers to the individual age of the number of unimodal matching (see methods)

Fig. 1. Effect of age on the distribution of silent-visual gestures according to the maternal visual attention for each individual (N=11). The effect of weighted mean age on the use of silent-visual gestures according to the maternal visual attention was significant (Spearman rank order correlation coefficient, p-value = 0.0001, r= +/-0.90).

Fig. 2. Number of silent-visual gestures for each individual with respect to maternal visual attention for infant (A; N=3), juvenile (B; N=4), and adolescent (C; N=4) chimpanzees. The lines illustrate individual shifts in behaviour across the two discrete levels of the attention condition.

Fig. 3. Variation in use of audible-or-contact signals and silent-visual gestures with respect to maternal visual attention by age category (**N=11,** *P<0.05. ***P<0.001). The deviations above and below the zero-line show changes (plus standard error bar) in the use of each modality, according to the maternal state of attention prior to gesturing, from the overall average use of that modality in gesturing.

Fig. 4. Proportion of audible and contact gestures used when the mother was visually inattentive (**N=11,** *P<0.05, **P<0.01, ***P<0.001). Large black circles represent mean proportion per subject. Median (horizontal lines), quartiles (boxes), percentiles (2.5% and 97.5%. vertical lines) and outliers (small black circles) are indicated. Differential use patterns are compared from one age category to another.

Fig. 5. Developmental trajectories of sensitivity to the recipient's attention state by chimpanzees' age category on the full sample of gestures.

Fig 1.

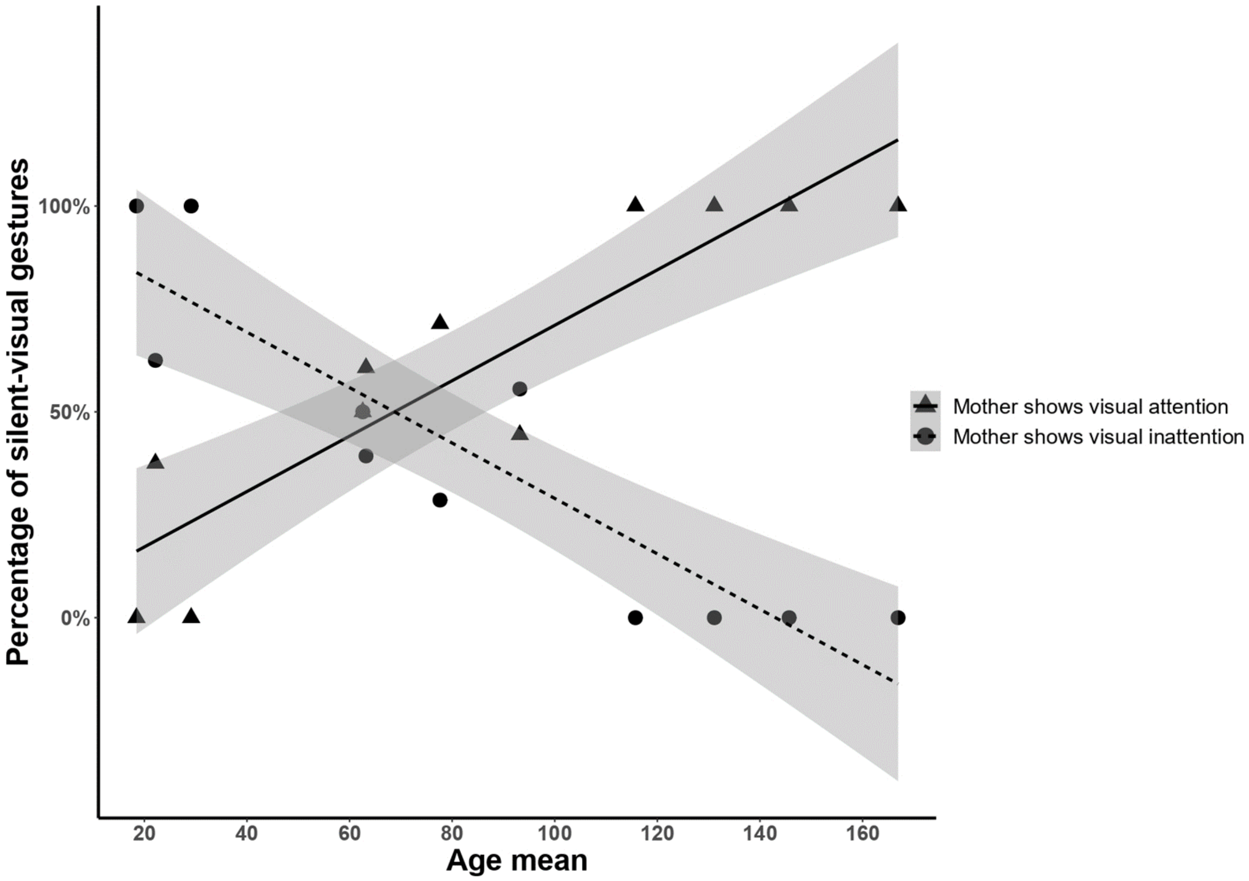

Percentage of silent-visual gestures
100%
50%
0%
20
40
60
80
100
120
140
160
Age mean
Mother shows visual attention
Mother shows visual inattention

Fig 2.

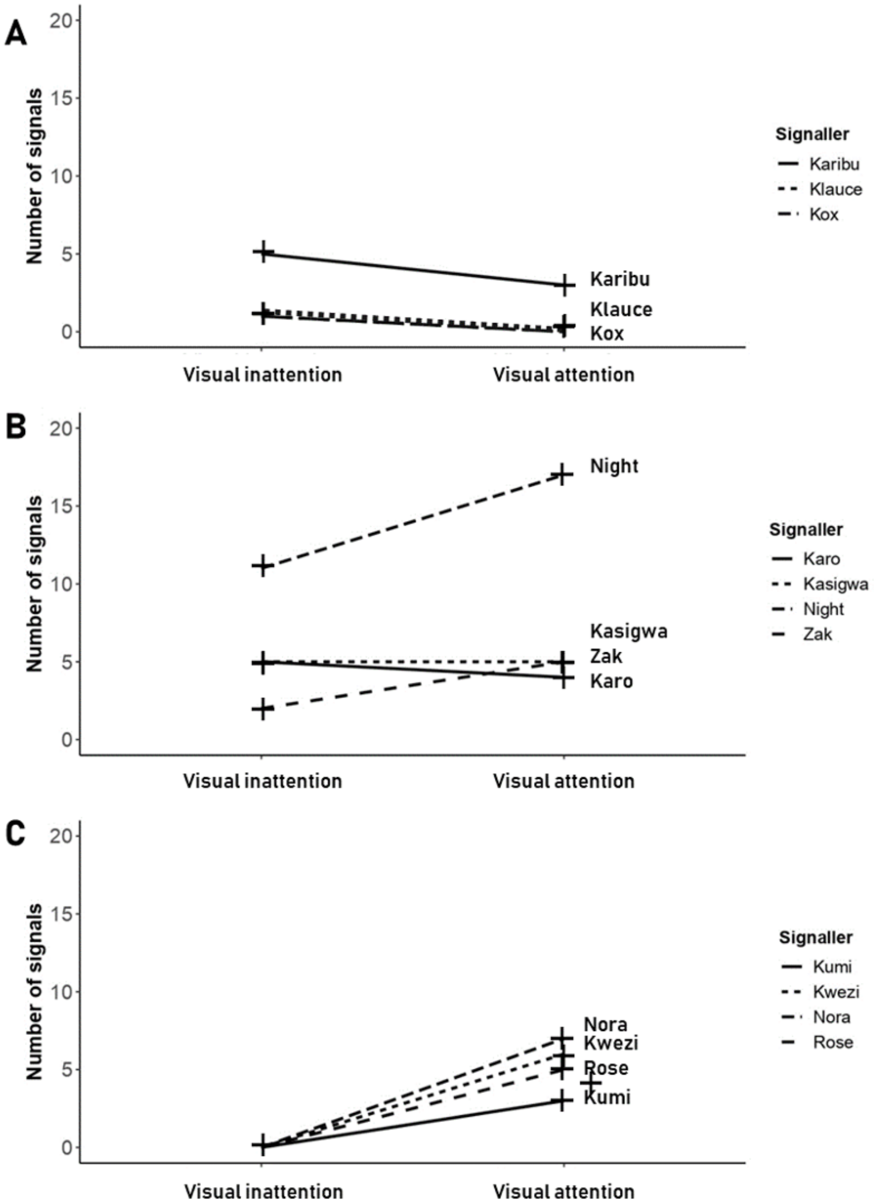

A
B
C
Number of signals
0
5
10
15
20
Visual inattention
Visual attention
Signaller
Karibu
Klauce
Kox
Karo
Kasigwa
Night
Zak
Kumi
Kwezi
Nora
Rose

Fig. 3

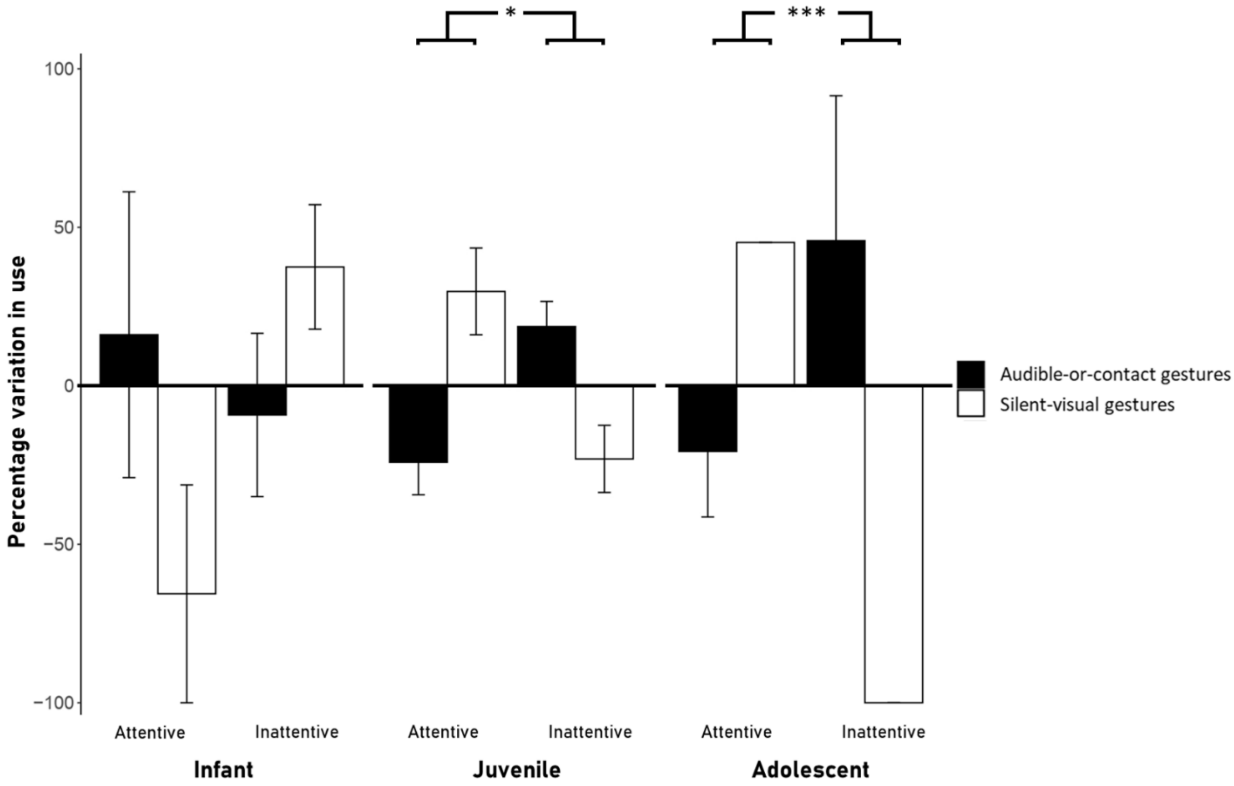

*
***
100
50
0
−50
−100
Percentage variation in use
Audible-or-contact gestures
Silent-visual gestures
Attentive
Inattentive
Attentive
Inattentive
Attentive
Inattentive
Infant
Juvenile
Adolescent

Fig 4.

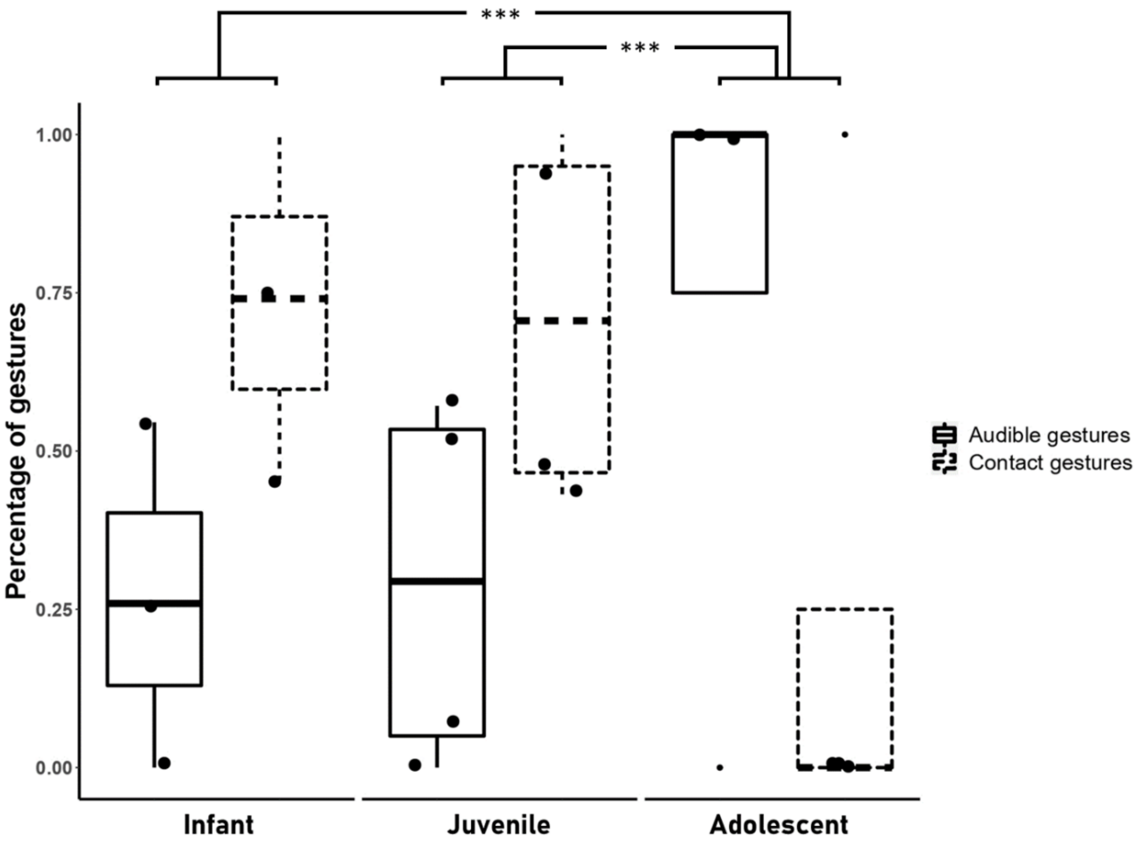
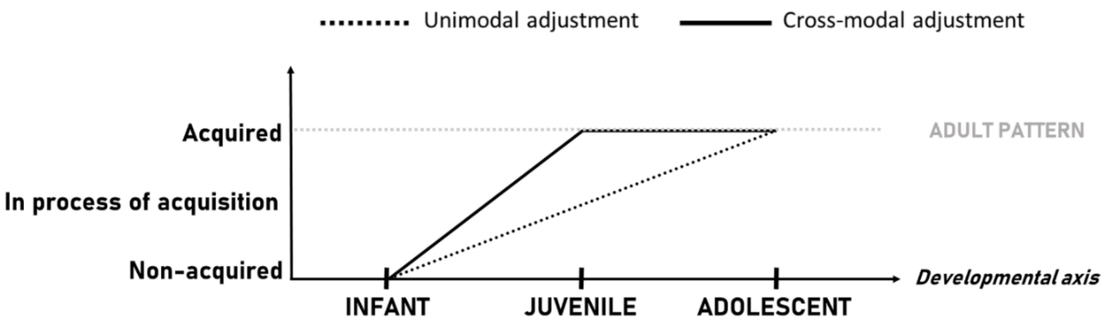

***
***
1.00
0.75
0.50
0.25
0.00
Percentage of gestures
Audible gestures
Contact gestures
Infant
Juvenile
Adolescent

Fig 5.


Unimodal adjustment
Cross-modal adjustment
Acquired
In process of acquisition
Non-acquired
ADULT PATTERN
Developmental axis
INFANT
JUVENILE
ADOLESCENT