1. Keven and Akins

2. Word counts: abstract 60; main text 1000; references 532; entire text 1846

3. Title: Beyond aerodigestion: exaptation of feeding-related mouth movements for social communication in human and non-human primates

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10. Abstract

Three arguments are advanced from human and non-human primate infancy research for the exaptation of ingestive mouth movements (tongue-protrusion and lip-smacking) for the purposes of social communication: Their relation to affiliative behaviours; their sensitivity to social context; and their role in social development. Although these behaviours may have an aerodigestive function, such an account of their occurrence is only partial.

11. Main text

Keven and Akins view infant mouth movements such as tongue protrusion (TP), as part of the system for regulating ingestion in relation to breathing. They view these behaviors as stereotyped, not goal-oriented, and unresponsive to stimulation, albeit varying with arousal. In contrast, we present three arguments from research on early parent-infant relationships, including cross-species and clinical samples, for the social function of such mouth movements: their relation to affiliative behaviors; their sensitivity to social context; and their role in social development.

Relationship between aerodigestive and affiliative behaviours. Observational studies of human and non-human primate (NHP) infants are remarkably consistent in showing that mouth movements originating in ingestion nevertheless have distinct, communicative, significance (Trevarthen, 1979; Van Hooff, 1962). These include TP in humans and lip-smacking (LS) in rhesus macaques. In each case, the behaviour rapidly becomes prominent in early parent-infant interactions (Trevarthen, 1974; Ferrari, Paukner, Ionica, & Suomi, 2009), and is highly organized, systematically co-occurring with other, clearly affiliative, behaviors. For instance, in humans, TP in the first two months is associated with smiling, wide mouth-opening and positive vocalizations, a cluster of expressions termed 'prespeech' (Figure 1a). These expressions occur during direct gaze to the adult's face, often accompanied by arm waving with open hand movements (Figure 1b) (Trevarthen, 1974; 1979; Lavelli & Fogel, 2002; 2005; 2013, SI). In macaques, LS similarly appears as part of social encounters, and co-occurs with direct gaze and proximal contact with the parent; even newborns actively solicit their mothers to interact with spontaneous LSs (Ferrari et al., 2009; Dettmer, et al., 2016). The time course of these expressions is strikingly similar in humans and monkeys, increasing in frequency over the first few weeks, and then declining with the reduction in face-to-face interactions and the infant's growing exploration (Trevarthen & Aitken, 2001; Ferrari et al., 2009). Notably, each behaviour is functionally autonomous with respect to digestive chewing- whether in terms of its co-occurrence (TP (SI1)), or developmental trajectory (LS (Ghazanfar & Takahashi, 2014).

a)

b)

Figure 1a and b: Infant TP, with and without arm/hand movements, during face-to-face interaction

Sensitivity to social context. Infant TP and LS are highly sensitive and responsive to others' interactive behavior. In addition to the consistent evidence from well-conducted studies for neonatal imitation of these gestures (Simpson, Murray, Paukner, & Ferrari, 2014), human research using experimental perturbations shows that if normal face-to-face contact is broken by the parent adopting a still, blank, face, infants show less positive social engagement (Mesman, van IJzendoorn, & Bakermans-Kranenburg, 2009), including reduced TP (Murray & Trevarthen, 1985). This effect is not simply a function of lack of parental stimulation lowering infant arousal, since similar reductions in engagement (and TP) occur when infants see their parent in a non-contingent vs. identical contingent face-to-face interaction (Murray & Trevarthen, 1985; Nadel, Carchon, Kervella, Marcelli, & Reserbat-Plantey, 1999). Disturbances in clinical populations also demonstrate the influence of variations in face-to-face interactions on human infants' social responses. For example, two-month-olds of socially anxious mothers show low levels of social engagement themselves, including TP, an effect that is mediated by their mothers' reduced positive social signals (Murray, Cooper, Creswell, Schofield, & Sack, 2007). Similar effects are found for infants of depressed mothers (Murray, Fiori-Cowley, Hooper, & Cooper, 1996). Parallel findings to the human experimental studies emerge from non-human primate research: specifically, infant macaques reduce their LS and social attention when presented with a still face vs. an active interactive experimenter; and they show more LS and attention when an experimenter interacts with them using contingent, imitative, mouth responses rather than similarly prominent, but non-contingent, repetitive mouth movements, despite the latter condition providing more overall stimulation (Sclafani, Paukner, Suomi, & Ferrari, 2014).

Role of infant TP and LS in later social development. Human observational studies show that parents respond positively to early infant signs of social engagement or 'prespeech', imitating and affirming them, and according them communicative and playful significance (Trevarthen, 1979; Lavelli & Fogel, 2002; SI). In turn, the further development of these infant behaviours is promoted by parental facial responsiveness, so that cultural differences in its prevalence (e.g., as between US/European and some African populations) predict somewhat different infant social trajectories (Kartner, Keller, & Yovsi, 2010; Wormann, Holodynski, Kartner, & Keller, 2012). Face-to-face interactions between mother and infant macaques also influence the development of infant social functioning: Monkey neonates that receive more facial responsiveness from their mothers spend more time in social contact with other monkeys at 2 months of age, and they initiate more social interactions at 5 months (Dettmer et al., 2016). That this effect is driven by experience of face-to-face interactions, rather than physical contact, is indicated by the finding that nursery-reared infants receiving mutual gaze and LS from a human caregiver subsequently show more social interest and social contact with peers than infants receiving either handling without gaze and LS, or standard nursery care. Notably, infant experience of early social interactions influences putative mirror neuron system responses, with infant monkeys raised with their biological mothers already demonstrating more mu desynchronization during observation of LS at three days postpartum compared to those raised apart (Vanderwert, Simpson, Paukner, Suomi, Fox, & Ferrari, 2015). Such impact suggests a preparedness of the neonate brain to respond to social cues by harnessing aerodigestive behaviours, with a rudimentary mirror system rapidly refined by early experience. This may increase neural sensitivity to socially relevant stimuli such as LS, and thereby confer significant benefits for infants'

navigation of the complex social world into which they are born (Vanderwert et al., 2015). Recent research with human children similarly suggests mirror system involvement in the processing of facial expressions from a young age (Rayson, Bonaituto, Ferrari, & Murray, 2016).

In sum, we provide evidence from naturalistic, experimental and clinical studies to show that infant mouth movements like TP/LS are complex and sensitive to context, and are fundamentally embedded in social interactions early in development, with longer-term significance for social functioning. Therefore, while both TP/LS may indeed have fundamental aerodigestive origins, they have also been exapted for uniquely social purposes.

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