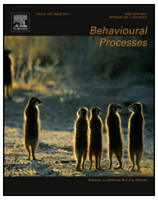
Behavioural Processes 115 (2015) 109–116

Contents lists available at ScienceDirect

Behavioural Processes

journal homepage: www.elsevier.com/locate/behavproc



Individual and population-level sex-dependent lateralization in yellow-legged gull (*Larus michahellis*) chicks

Maria Romano[a], Marco Parolini[a,*], Manuela Caprioli[a], Caterina Spiezio[b], Diego Rubolini[a], Nicola Saino[a,**]

[a] *Department of Biosciences, University of Milan, via Celoria 26, I-20133 Milan, Italy*
[b] *Research and Conservation Department, Parco Naturaviva, Verona, Italy*

ARTICLE INFO

Article history:
Received 2 March 2015
Received in revised form 21 March 2015
Accepted 23 March 2015
Available online 25 March 2015

Keywords:
Begging behavior
Heritability
Larus michahellis
Lateralization
Laying order
Maternal effects
Sex
Stress

ABSTRACT

Behavioral lateralization at the population level is widespread across vertebrates, with considerable variation among species. However, evidence for individual-level and sex-dependent lateralization is sparse and inconsistent in fish, reptiles and birds. In addition, covariation of lateralization with position in the laying sequence, which is expected because the concentration of maternal egg hormones varies with laying order, has never been investigated. We analyzed lateralization of yellow-legged gull (*Larus michahellis*) chicks in reverting from supine to prone posture ('RTP' response) and in pecking at a dummy parental bill to solicit food provisioning ('begging' response). Chicks were lateralized both at the population and at the individual level in the RTP response and at the individual level in begging. Lateralization in the RTP was sex-dependent, as females showed a leftward preference. Lateralization in either motor task was not correlated within individuals. Lateralization did not differ among families, suggesting little additive genetic variation. Lateral preference in begging response varied according to laying order and matched variation in egg androgens concentration. Our study confirms previous findings on population-level lateralization and adds to the scant information on individual-level and heritable variation in lateralization in birds. Moreover, it hints at epigenetic components in lateralization depending on maternal effects.

1. Introduction

Behavioral lateralization is the different use of either side of the body determined by brain hemispheric asymmetry and functional specialization (Güntürkün et al., 2000; Ventolini et al., 2005). Lateralization of the brain and of behavior was thought to be unique for long to humans, but over the past 30 years evidence has been accumulating that the brain of vertebrates exhibits anatomical and functional asymmetries, and that motor and sensory directional lateralization at the population level are relatively common (see Halpern et al., 2005; Rogers et al., 2013).

Besides humans (Annett, 2006; Perelle and Ehrman, 1994; Raymond and Pontier, 2004), preferential limb use in specific tasks is now well-known in other mammals (e.g., mice, rats, bats and wallabies; Collins, 1975; Giljov et al., 2012; Stashkevich and Kulikov, 2007; Zucca et al., 2010) and birds (e.g., parrots, crows and chickens; Brown and Magat, 2011; Hunt et al., 2001; Izawa et al., 2005; Mench and Andrew, 1986; Rogers and Workman, 1993; Rutledge and Hunt, 2004). Parrots and cockatoos, for example, show significant footedness in manipulating food and objects (Harris, 1989; Rogers, 1980; Rogers and Workman, 1993).

Behavioral lateralization in a population may in fact occur at two different levels. Most individuals may display similar, consistent lateralization, resulting in directional lateralization at the population level ("population-level lateralization") with no inter-individual variation in use of either side of the body. This would be the case if all individuals consistently show a similar pattern of lateralization, both in extent and side, which does not vary among individuals. On the other hand, lateralization can vary among individuals ("individual-level lateralization"), with some showing either left- or right-bias in lateral preference, or different extent of lateral preference for either side (Rogers, 2002; Vallortigara and Rogers, 2005). The two forms of lateralization may occur together, and whether individual-level lateralization will result in lateralization at the population level depends on the frequency of individuals which show directional preference for either side.

---

* Corresponding author.
** Corresponding author. Tel.: +39 02 503 14808; fax: +39 02 503 14713.
E-mail addresses: marco.parolini@unimi.it (M. Parolini), nicola.saino@unimi.it (N. Saino).

http://dx.doi.org/10.1016/j.beproc.2015.03.012
0376-6357/

Behavioral lateralization at the level of bird populations has been reported in several studies. For example, species from diverse orders are known to preferentially use their right eye while searching for food (Mench and Andrew, 1986; Rogers et al., 2004) and discriminating between food and non-food items (Alonso, 1998; Güntürkün et al., 2000; McKenzie et al., 1998; Rogers et al., 2007; Valenti et al., 2003; Ventolini et al., 2005). In Caspian terns (*Hydroprogne caspia*), during successful events of prey delivery to the chicks bill, parental head's position is more often oriented rightwards. Moreover, parents switch prey orientation significantly more often from left to right than the reverse (Grace and Craig, 2008). Domestic chicken chicks more frequently use the left rather than the right eye when pecking at strangers (Vallortigara et al., 2001; Zucca and Sovrano, 2008). Quails (*Coturnix* sp.) turn leftwards when viewing a stranger and rightwards when viewing a companion. Australian magpie (*Gymnorhina tibicen*) chicks are more likely to beg for food on the right side of the attending parents (Hoffman et al., 2006). In addition, Australian parrot species favor the left or right foot to manipulate objects (Magat and Brown, 2009; Brown and Magat, 2011) and New Caledonian crows (*Corvus moneduloides*) are more likely to use their right eye in tool making and use (see Hunt, 2000a,b,b).

Information on individual-level lateralization in birds, however, is relatively scant. For example, individual New Caledonian crows are lateralized in tool grasping but the direction of lateralization was found to vary among individuals (Rutledge and Hunt, 2004; Vallortigara and Rogers, 2005). Caribbean flamingos (*Phoenicopterus ruber*) are individually lateralized in neck turning for resting (Anderson et al., 2009) as well as in feeding behavior (Peluso and Anderson, 2014).

The extent of genetic versus epigenetic/environmental components in individual-level lateralization is a still largely unresolved issue (Annett, 1978; Bishop, 2001; Laland et al., 1995; Provins, 1997). Heritability studies in humans point at significant additive genetic variation (Rife, 1940; Denny and O'sullivan, 2007; Llaurens et al., 2009), while also suggesting that realized heritability can vary depending on environmental effects (Schaafsma et al., 2009). In addition, evidence exists that lateralization may be sex-dependent (McManus, 2002). For example, in different avian species, sex differences in the direction and strength of lateralization have been documented, with males being more strongly lateralized in the use of either eye in cognitive tasks compared to females (Adret and Rogers, 1989; Alonso, 1998; Güntürkün, 1997; Regolin and Vallortigara, 1996; Rogers, 1997; Vallortigara et al., 1996). Differences in steroid hormone profile between the sexes have been invoked as proximate drivers of sex-dependent lateralization, as also suggested by an effect of experimentally altered exposure to prenatal testosterone on right-hemisphere dominance (see review in Pfannkuche et al., 2009). However, evidence for genetic and sex-dependent variation in lateralization is inconsistent, and few models of the genetic control of variation in lateralization have been successfully built (see Schaafsma et al., 2013).

Environmental effects, including the pre-natal intra-uterine or egg conditions, may contribute to variation in individual lateralization. In birds, prenatal conditions may influence post-natal lateralization because of the asymmetric position of the avian embryo and larger light stimulation of the right eye which points toward the semi-transparent eggshell (Kuo, 1932; Rogers and Bolden, 1991; Güntürkün et al., 1998; Manns and Güntürkün, 1999; Rogers and Deng, 1999; Koshiba et al., 2003). In addition, postural asymmetry inside the egg may cause motor lateralization in post-hatching life because of differential use of either leg to maintain postural and positional control before hatching or to escape from the eggshell (Rogers and Workman, 1993). Pre-hatching postural asymmetry may thus result in consistent directional lateralization at the individual and population levels, owing to almost complete invariance of postural asymmetry of avian embryos at least in species for which information is available (Nicola Saino, personal observation on the yellow-legged gull, *Larus michahellis*).

A wide class of pre-natal environmental influences on lateralization may arise as a consequence of 'maternal effects' (Mousseau and Fox, 1998). Transmission to the egg of maternal substances with developmental and organizational effects may affect the development of lateralization. Steroid hormones are delivered by the mother to her eggs in amounts that may vary among mothers as well as according to position of individual eggs in the laying sequence or sex of the individual offspring. Corticosterone, which occurs both in the avian yolk and albumen (Rubolini et al., 2005, 2011), affects the development of visual asymmetry. Elevated levels of corticosterone during the sensitive period just before hatching influence the development of visual asymmetry which may be absent or vary randomly among individuals before the sensitive period (Rogers and Deng, 2005). Development of asymmetry in visual pathways has important functional effects by altering, for example, chick response to predators (Freire et al., 2006). In addition, studies where the concentration of egg hormones (testosterone, estrogens, and corticosterone) was manipulated have shown that hormone treatment reduces the degree of visual lateralization but does not change its direction (see Pfannkuche et al., 2009). Egg androgens and oestrogens are also known to affect visual lateralization (see Pfannkuche et al., 2009). The effects of maternal egg hormones may combine with endogenous hormones produced by the developing embryo. Variation in the egg hormonal milieu both at the among-clutch level and at the within-clutch level according to for example laying order and embryo sex, and differential susceptibility of male and female embryos to steroid hormones, leads one to expect complex patterns of variation in lateralization among broods as well as among siblings. Because the patterns of variation in egg composition are species-specific, any covariation in lateralization depending on sex and laying order should vary idiosyncratically among species.

In the present study of a semi-precocial bird, the yellow-legged gull, we mostly focus on the analysis of variation in lateralization in two different motor tasks (solicitation of food provisioning by pecking at a dummy parental head, and reverting from supine to prone position) at the population and family levels, as well as within families according to sex and position of the original egg in the laying sequence. Specifically, in repeated trials on the same set of newly hatched chicks in the field we first tested whether individuals were consistent in the side on which they performed the solicitation display ('begging display') and the Reversal-To-Prone (RTP) response, indicating lateral preference at specific tasks. We then tested whether significant lateralization occurred at the population level, but also at the family level, by testing for significant resemblance among siblings in the frequency of leftwards or rightwards begging pecks and RTP responses. Significant lateralization at the family level was intended as suggestive of heritable variation in lateralization. The behavioral tests were performed very early after hatching, so that post-natal social effects such as learning and parental behavior on displayed lateralization were likely minimal (begging tests) or nil (RTP test; see also Methods). Admittedly, we could not account for any effect of prenatal environment caused by similarity in the quality of the eggs laid by the same mother on resemblance in lateralization among siblings. Such early maternal effects are typically extremely difficult to control for experimentally. Estimates of variance in lateralization at the family level therefore represent the upper limit of heritability, as they also account for shared early-maternal effects due to resemblance in the quality of sibling eggs. Finally, we analyzed variation in lateralization according to the independent and combined effects of sex and laying order of the original egg. We predicted that displayed lateralization varied according to laying order because egg androgens