Neuroscience 354 (2017) 54–68

DYNAMIC FEATURES OF ANIMATE MOTION ACTIVATE SEPTAL AND PREOPTIC AREAS IN VISUALLY NAÏVE CHICKS (*GALLUS GALLUS*)

ELENA LORENZI,* UWE MAYER ORSOLA ROSA-SALVA AND GIORGIO VALLORTIGARA

Center for Mind/Brain Sciences, University of Trento, Piazza Manifattura 1, 38068 Rovereto (TN), Italy

Abstract—The septum is an evolutionarily well-conserved part of the limbic system. It is known to be involved in many aspects of social behavior and is considered a key node of the social behavior network, together with the preoptic area. Involvement of these two brain regions has been recently observed in newly hatched chicks exposed to the natural motion of a living conspecific. However, it is unknown whether these areas respond also to simple motion cues that elicit animacy perception in humans and social predispositions in chicks. For example, naïve chicks are attracted by visual objects that appear to spontaneously change their speed (an index of self-propulsion, typical of animate creatures). Here we show that the right septum and the preoptic area of newly hatched visually naïve chicks exposed to speed changes have higher neuronal activity (revealed by c-Fos expression), compared with that of chicks exposed to constant motion. We thus found an involvement of these two areas in the perception of motion cues associated with animacy in newly hatched chicks without any previous visual experience. This demonstrates their early involvement in processing simple motion cues that allow the detection of animate creatures and elicit social predispositions in this animal model, as well as preferential attention in human infants and the perception of animacy in human adults.

Key words: septum, c-Fos, social predispositions, animate motion, avian, animacy.

INTRODUCTION

The detection of animate creatures, such as conspecifics, preys or predators, is crucial for survival and can be based on dynamic cues typical of animate motion, as opposed to that of inanimate objects (for a review see Rosa-Salva et al., 2015). Studies conducted in visually naïve chicks (*Gallus gallus domesticus*), human newborns and infant monkeys demonstrated similar preferences for stimuli displaying both static and dynamic cues of animacy (Sugita, 2008; Simion et al., 2008; Mascalzoni et al., 2010; Rosa-Salva et al., 2010, 2011, 2012a; Versace et al., 2016, 2017). These social predispositions are active since birth and, at least in animal models, emerge in the absence of any specific learning experience. One of the adaptive functions of social predispositions might be to guide the action of learning mechanisms (e.g., filial imprinting) toward appropriate social objects, channeling the subsequent development of neural mechanisms specialized for sophisticate processing of social information (Johnson, 2005; Rosa-Salva et al., 2015; Di Giorgio et al., 2016a,b; Versace and Vallortigara, 2015; Miura and Matsushima, 2016).

The present study focuses on responses to specific features of animate motion. Naïve chicks and human newborns show a preference for point-light displays depicting semi-rigid biological motion, in which some points maintain always a fixed distance between each other, but vary their distance with respect to other points, the typical gait pattern of legged animals (Vallortigara et al., 2005; Vallortigara and Regolin, 2006; Simion et al., 2008; Miura and Matsushima, 2012). Animate motion can also be recognized because it is self-propelled, revealing the presence of an internal energy source to the moving object. Different motion patterns associated with self-propulsion increase the perception of animacy in human observers (Tremoulet and Feldman, 2000) and are preferred by newborn babies (Di Giorgio et al., 2016c), infants (Frankenhuis et al., 2013) and domestic chicks (Mascalzoni et al., 2010; Rosa-Salva et al., 2016). Recently we investigated naïve chicks' responses to speed changes, another index of self-propulsion. We found a spontaneous preference for a simple object that autonomously changes its speed, accelerating and then decelerating, to an identical one that moves at constant velocity. The preference disappeared when the two moments in which the object was changing speed were occluded from view, indicating that chicks were indeed responding to this visual cue (Rosa-Salva et al., 2016).

The neural correlates of these social predispositions are mostly unknown. We are conducting a series of experiments to investigate this issue in chicks, by mapping neuronal activities through immediate early genes expression (Mayer et al., 2016a,b; Mayer et al., 2017a). This methodology is commonly used as a marker of neuronal activation in different species, including birds

*Corresponding author.
E-mail addresses: elena.lorenzi@unitn.it (E. Lorenzi), uwe.mayer@unitn.it (U. Mayer), orsola.rosasalva@unitn.it (O. Rosa-Salva), giorgio.vallortigara@unitn.it (G. Vallortigara).

Abbreviations: IMM, intermediate medial mesopallium; -ir, immunoreactive; PBS, phosphate-buffered saline; PFA, paraformaldehyde; POA, preoptic area; TnA, nucleus taeniae.

http://dx.doi.org/10.1016/j.neuroscience.2017.04.022

(Sheng and Greenberg, 1990; Lanahan and Worley, 1998; Guzowski et al., 2005; Mayer and Bischof, 2012; Mayer et al., 2016a; Mayer et al., 2017a,b). In our studies, the static configuration of features or the natural motion typical of conspecifics stimulated differential activation in the intermediate medial mesopallium (IMM), as well as in the amygdaloid, septal and preoptic areas (Mayer et al., 2016b; 2017a,b).

As regards the first structure, IMM is involved in filial imprinting learning (Horn, 1979; Bolhuis, 1991; Ambalavanar et al., 1993; McCabe and Horn, 1994; Horn, 1998, 2004; McCabe, 2013). Although IMM is not needed for the expression of predispositions (Horn and McCabe, 1984), we found differential activation of this region after approach to a stimulus whose static configuration of features respects that of a social companion (stuffed hen) compared to a scrambled version of it (Mayer et al., 2016b).

Interestingly, the other three areas identified in our previous studies (septal, amygdaloid and preoptic nuclei) are implicated in adult social behaviors, being part of the so-called "social decision making network" (O'Connell and Hofmann, 2011; see also Balthazart et al., 1998a,b; Gahr, 2001 for the avian preoptic area). This network is shared among all vertebrates and comprises the social behavior network (Newman, 1999; Goodson, 2005), consisting of interconnected areas rich in sex steroid receptors, and the mesolimbic reward network (O'Connell and Hofmann, 2011).

Septum is a well-conserved part of the limbic system in all vertebrate groups (Northcutt, 1981; Puelles et al., 2000), it is vertically traversed by the tractus septopalliomesencephalicus, which connects the visual Wulst with the optic tectum (Karten et al., 1973), it receives important connections from hippocampus and it is interconnected with preoptic area and arcopallium (Montagnese et al., 2004, 2008; Xin et al., 2016). Septum is involved in multiple social functions. In mammals it has been implicated in agonistic and mating behavior (Kollack-Walker and Newman, 1995, 1997), in pair bonding (Liu et al., 2001), in dominance hierarchies (Ferris et al., 1990) and in attack-defense responses (Albert and Chew, 1980). In birds, it is involved in sexual behavior (Taziaux et al., 2006), gregariousness (Goodson et al., 2009; Kelly and Goodson, 2014), songbirds' vocalizations, aggressive and submissive behaviors (Goodson, 1998; Nishizawa et al., 2011). The avian preoptic area (POA) of the hypothalamus plays a conserved role in aggression, parental care, male sexual behavior as well as in appetitive and consummatory behavior (Akerman et al., 1960; Balthazart et al., 1990, 1998a; Slawski and Buntin, 1995; Riters et al., 1998; Ruscio and Adkins-Regan, 2004; Taziaux et al., 2006, 2008; Bharati and Goodson, 2006).

Finally, the amygdala has been theorized to support early social responses in humans (e.g., attention to faces, Johnson, 2005). The mammalian amygdala has been implicated, among other things, in fear responses (Hamm and Weike, 2005), olfactory social communication (Petrulis, 2009), maternal behavior (Sheehan et al., 2001) and innate reproductive and defensive behaviors (Choi et al., 2005). Avian homologs for mammalian amygdala are still debated (Cheng et al., 1999; Reiner et al., 2004; Jarvis et al., 2005; Yamamoto and Reiner, 2005; Yamamoto et al., 2005; Martínez-García et al., 2008). The nucleus taeniae (TnA), in the posterior and medial arcopallium, is considered homolog to the subpallial, medial amygdala (Cheng et al., 1999; Yamamoto and Reiner, 2005; Yamamoto et al., 2005). Homologies for the pallial amygdala are more controversial, but most agree that at least part of the arcopallium is homolog to the pallial amygdala (Butler et al., 2011). In birds, the arcopallial region is involved in agonistic behavior (Phillips and Youngren, 1971) and fear responses (Phillips, 1968; Martin et al., 1979). TnA is also implicated in sexual behavior (Thompson et al., 1998; Ikebuchi et al., 2009). In an altricial species, the zebra finch, TnA can already be delineated at post-hatching day one (Ikebuchi et al., 2012), suggesting that its early development may be involved in early social control.

Given the importance of these areas for social functions in adult animals, it is surprising that so far very few studies investigated their involvement in early social behaviors of newborn animals. Early social behaviors are crucial for the ontogenesis of social cognition (Johnson, 2005; Sugita, 2008; Di Giorgio et al., 2016b). In our recent studies, arcopallium responded to the first exposure to an alive conspecific compared to baseline (i.e., exposure to an empty chamber Mayer et al., 2017a). However, this area did not show a difference between chicks exposed to a living conspecific and those exposed to a taxidermized individual of identical appearance rigidly rotating on its axis (Mayer et al., 2017b). This suggests that arcopallium could be more responsive to the static features that characterize conspecifics than to their motion. On the contrary, septum was activated in both studies (Mayer et al., 2017a,b). Finally, while POA was not investigated in the first study, this area showed higher activity in response to the natural motion of the living chick, compared to the rotating one (Mayer et al., 2017b). This suggests that these two areas should be sensitive to the type of natural motion emitted by a live conspecific. However, it remains unclear which features of the motion of the alive conspecific (e.g., semi-rigidity, speed changes, starts from rest etc.) elicited the effect and whether any of these motion features presented in isolation would be sufficient to activate septum and POA, if displayed by an agent whose morphology does not resemble that of conspecific. In the current study, we thus compared brain activation (immediate early gene expression) in septum, POA, arcopallium and IMM of visually naïve chicks exposed either to a stimulus characterized by speed changes or to a control constant-speed stimulus (stimuli from Rosa-Salva et al., 2016). This allowed us to use very well controlled stimuli to test the neural correlates of chicks' social predispositions for animate motion cues.

MATERIALS AND METHODS

Subjects

Subjects were 24 domestic chicks (*Gallus gallus domesticus*). The "Hybro strain", a local variety derived

from the White Leghorn breed, was used. We obtained fertilized eggs from a local commercial hatchery (Agricola Berica, Montegalda (VI) – Italy). Eggs were incubated within a Marans P140TU-P210TU incubator at a temperature of 37.7 °C, with 60% humidity. The incubator was kept in darkness, preventing any visual experience during incubation and hatching.

Apparatus

The test apparatus (Fig. 1A) was a white corridor (85 × 30 × 30 cm) with two video screens (LCD Monitor BenQ XL2410T) at its ends. One screen placed at one side of the corridor showed one of the stimuli (which one depended on the experimental condition). The second screen remained off, its presence serving only to counterbalance the visual appearance of the two sides of the corridor. The corridor was divided in three sectors: a central sector (45 cm long), and two identical lateral choice sectors (each 20 cm long), comprising the area directly in front of the two screens. Two steps (1.5 cm high) delimited the central sector. The animals were positioned in the centre, to enter the lateral sector and approach the stimulus chicks had to climb on one of the two steps. A video-camera was placed above the apparatus, recording animals' behavior. It was connected to a monitor screen in the same room, enabling the experimenter to monitor the behavior on-line. Only the screen playing the video-stimulus illuminated the apparatus.

Stimuli

The stimuli were identical to those used in a previous study, in which they were employed to successfully demonstrate a spontaneous preference for speed changes in naïve chicks (Rosa-Salva et al., 2016). They consisted of two video-animations representing the movement of a simple object (created with MATLAB R2012b with Psychtoolbox-3 extensions, Kleiner et al., 2007). Each stimulus represented a red disk (diameter 3 cm) moving linearly on a dark background (see Fig. 1B, C). The portion of the screen visible to the subject within the apparatus (30 cm long) was framed, from the sides and from the bottom, by a gray U-shaped digital figure: two lateral walls (each 2.5 cm) and a floor over which the red object was moving (the visible trajectory of the red object motion was thus 24.6 cm long). The red object always entered the observer's view already in motion, appearing from behind one of the lateral gray walls, which acted as digital occluders. Similarly, once completed its motion, the red object disappeared while still in motion, slipping behind one of the lateral gray walls and appearing again after one second of delay. The motion of the red object continued in a loop for six minutes, the entire duration of the behavioral procedure.

The experimental stimulus (henceforth speed-change stimulus) displayed two visible speed changes during its motion, with a slow-to-fast speed ratio of 0.171. It abruptly accelerated from initial speed of 3.37 cm/s to 19.64 cm/s at one third of its trajectory and decelerated back to the initial speed at two thirds of the way

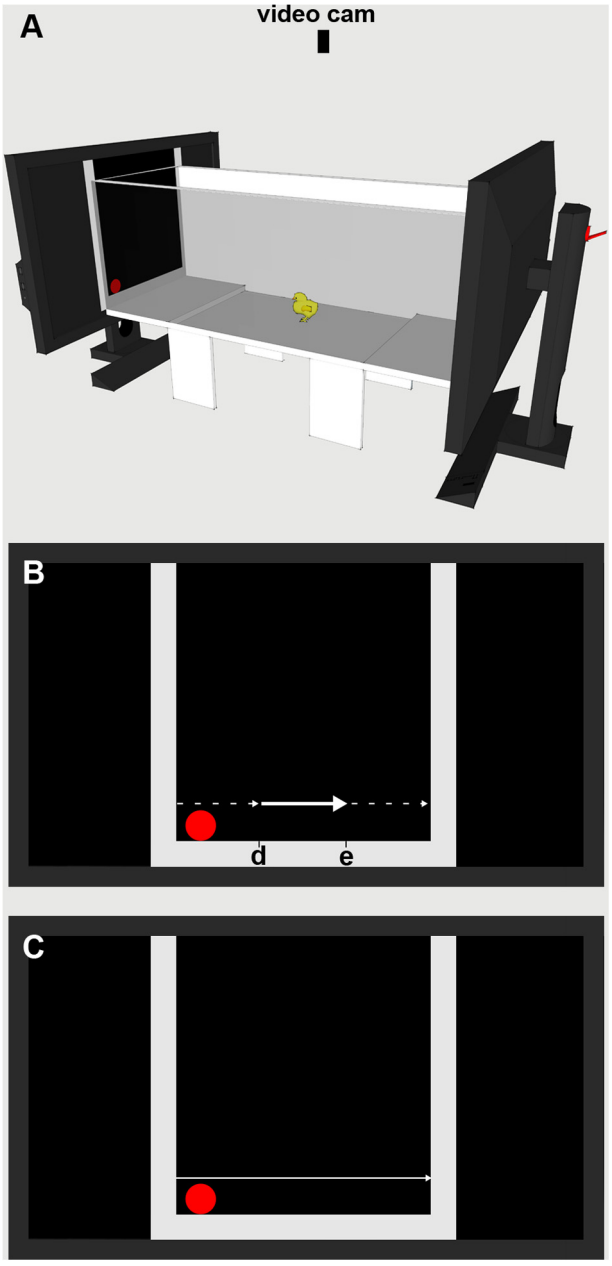

Fig. 1. Experimental setup. (A) Schematic representation of the test apparatus, for illustrative reasons one of the two long walls is depicted as if it were translucent. The stimulus was presented on one of the two identical screens at the ends of the runway. To approach the stimulus, chicks had to climb the step nearby the screen playing the stimulus. (B) Schematic representation of the speed-change stimulus that was increasing its speed at point *d* and decreasing it to initial velocity at point *e*. (C) Schematic representation of the control stimulus that was moving at constant speed.

(Fig. 1B). On contrary, the control stimulus (speed-constant stimulus) moved at a constant speed of 4.64 cm/s (Fig. 1C). Both stimuli moved at the same average speed.

Test session for c-Fos labeling

Chicks were tested individually during the first day after hatching. The animals were taken from the incubator in

complete darkness and transported, inside a closed dark box, to the experimental room. Each animal was placed in the middle of the central sector of the corridor (Fig. 1A), facing one of the two long walls (left–right orientation with respect to the long walls was counterbalanced between subjects). The chick could freely move inside the apparatus for the whole duration of the test (6 min). Doing so, it could spontaneously approach the screen with the stimulus. This involved climbing on the step on the stimulus side of the apparatus, which allowed a precise definition of a successful approach. Birds that failed to do so were excluded from further procedures. After the behavioral exposure, the subjects were carefully placed in the transportation box and carried back to the dark incubator, where they remained until perfusion. In order to distinguish individual subjects also in the darkness, but to keep the auditory environment as it was before, they were placed individually within the same incubator as the other chicks. Overall, we collected 12 experimental group chicks that approached the speed-changing stimulus and 12 control group chicks that approached the speed-constant stimulus. Two-to-six subjects were tested per week, equally subdivided in the two groups. In this way, the groups were always balanced with regard to the hatching batch and the staining procedure.

Immunohistochemistry

Seventy-five minutes after the end of the test, subjects were overdosed by an intramuscular injection of 0.05-ml Ketamine/Xylazine Solution (1:1 Ketamine 10 mg/ml + Xylazine 2 mg/ml) per 10 g of body weight. They were perfused transcardially with cold phosphate-buffered saline (PBS; 0.1 mol, pH = 7.4, 0.9% sodium chloride, 5 °C) and paraformaldehyde (4% PFA in PBS). The skull with the brain was transferred to 4% PFA, where it was post-fixed and stored until processing. To ensure correct orientation (45°) for the coronal sections, procedures described in the chick brain atlas of Kuenzel and Masson, 1988 were followed. The brains were then carefully removed from the skulls under a dissecting microscope. The left and the right hemispheres were separated and processed separately. Each hemisphere was covered with a 7% gelatine in PBS containing egg yolk (4.2 g gelatine + 60 ml PBS + 1 egg yolk at 40° C), after cooling they were post-fixated in 4% PFA/PBS/20% sucrose for approximately 48 h at 5 °C, and then transferred to 30% Sucrose/0.4%PFA/PBS for further 48–72 h. The brains were frozen at -80 °C in plastic molds, covered with O.C.T. (Tissue-Tek freezing medium). Six series of 40-μm coronal sections were cut on a Cryostat (Leica CM1850 UV) at −20 °C and collected in PBS. For free-floating immunostaining only the sections of the first series were used, whereas the other series were kept as backup. Between each of the following steps the sections were washed in PBS. After incubation in 0.3% H_2O_2/PBS for 20 min. the sections were treated for 30 min with 3% normal goat serum (S-1000, Vector Laboratories, Burlingame, CA). The first antibody reaction was carried out for 24-36 h at 5 °C on a rotator using c-Fos antibody in PBS solution (1:2000; rabbit, polyclonal K-25, Santa Cruz, CA) containing 0.1% Bovine Serum Albumin (BSA, SP-5050, Vector Laboratories). Sections were incubated in the secondary antibody reagent for 60 min at room temperature (biotinylated anti-rabbit in PBS, 1:200, BA- 1000, Vector Laboratories). The ABC kit (Vectastain Elite ABC Kit, PK-6100, Vector Laboratories) was used for signal amplification and the VIP kit (SK-4600, Vector Laboratories) for the visualization of the c-Fos containing neurons. After serial mounting on gelatine-coated slides, sections were dried at 50 °C and counterstained with methyl green (H-3402, Vector Laboratories). They were gradually dehydrated in ethanol (70%, 80%, 90%, 99% ethanol, for 3 min each then placed in xylene) and cover slipped with Eukitt (FLUKA).

Brain analysis

Brain sections were examined under a microscope at a magnification of 200x (Zeiss Axio Examiner) and a digital camera (Zeiss AxioCam MRc 5). Counting of the c-Fos immunoreactive (-ir) cells was performed blind to the experimental condition. Contrast and exposure time of the camera were adjusted so that the image on the screen (ZEN Imaging software, Zeiss) matched the view under the microscope. Successful immunostaining produced dark, purple-black stained nuclei, which were easily distinguishable from the non-activated cells, which were stained green (see Fig. 3). For counting, a rectangle enclosure $150 \times 250\ \mu m^2$, was placed over the different sample areas in a way such that it covered as many activated cells as possible while keeping a minimum distance from the border of a neighboring subdivision and the edge of the brain section. Every activated c-Fos-ir cell within each sample area was marked on the screen with the "event marker" of the ZEN software, which automatically computed the total number of marked c-Fos-ir cells. To estimate labeled cell density in septum two-to-eleven sections of each hemisphere were selected by the shape and anatomical landmarks that would correspond to the A(nterior)9.4 to A8.4 (Kuenzel and Masson, 1988). In fact, in the atlas the coordinates were estimated in two-week-old chicks, (average body weight 300–325 g). The newly hatched chicks used here weight about 46 g and have a different anterior coordinate. The septum of each section was parsed into six subdivisions: dorsal, dorso-lateral, dorso-medial, ventro-lateral, ventro-medial and medial portion of the ventro-medial septum. Typical placements of the counting enclosure are depicted in Fig. 2. To estimate labeled cell density in the intermediate medial mesopallium (IMM) we relied on previous descriptions of this region (Liu et al., 2001; Klatt and Goodson, 2013). McCabe and Horn (1994) report IMM to be located at the anterior coordinate A7.6 of the Kuenzel and Masson atlas (1988). Seven-to-eight brain slices, from a region where the shape of IMM was corresponding to that observed between A8.6 and A7.6 of Kuenzel and Masson (1988), were selected for the analysis. The rectangular enclosure was positioned inside IMM as in Ambalavanar et al. (1993), see also Fig. 2A. To estimate cell densities within the arcopallium and TnA, three-to-eight sections of both hemispheres were selected from

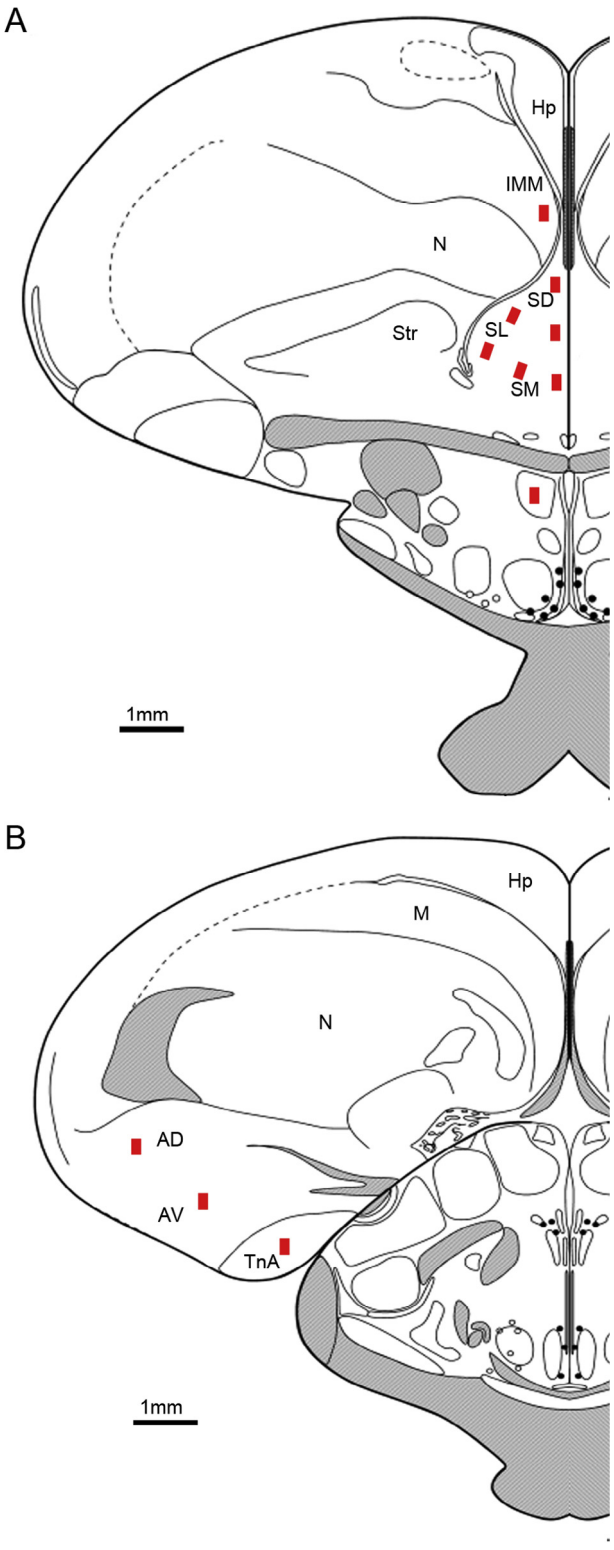

Fig. 2. Areas of interest. Schematic representation of two coronal sections (adapted from Kuenzel and Masson, 1988) showing the typical placements of the counting areas (red rectangles). (A) Counting areas within septum and preoptic area. (B) Counting areas in arcopallium. SD – dorsal septum, SL – lateral septum, SM – medial septum, Hp – hippocampus, IMM – intermediate medial mesopallium, M - mesopallium, N - nidopallium, Str-striatum, AD – dorsal arcopallium, AV – ventral arcopallium, TnA – nucleus taeniae. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

the region extending from A 7.6 to A 6.4 in Kuenzel and Masson (1988). Arcopallium is a telencephalic region delimitated in its upper boundary by the lamina arcopallialis dorsalis, whereas TnA in the ventral part can be visually distinguished by the different cell densities (see Fig. 2B). Recently, arcopallium has been reported to be functionally subdivided in medial and lateral regions (Xin et al., 2016). However, arcopallial subdivisions are still heavily debated in the literature (Reiner et al., 2004; Hanics et al., 2017). Our aim was not to investigate the internal subdivisions of this structure; thus, we took the most conservative approach (Karten and Hodos, 1967) and we parsed arcopallium into dorsal and ventral parts for counting (see Fig. 2B).

After completing the cell counts, the mean values derived from the sections were initially calculated for each of the subdivisions independently and cell densities were standardized to 1 mm^2. Cell counts, pooled from the six subdivisions in septum, were further averaged to estimate overall septal activity. Also, the cell counts pooled from the two subdivisions in arcopallium and the counting in TnA were averaged to estimate overall activity in this amygdala equivalent. This was done for the two hemispheres separately. The resulting individual bird means were considered overall indicators for the number of c-Fos-ir cells in the three regions of interest (septum, arcopallium, intermediate medial mesopallium) and were employed for further statistical analysis.

After the completion of the analyses of these three brain areas, we decided post hoc to additionally analyze data from a sub-region of the preoptic area, which showed responsivity to natural motion in another study from our lab (Mayer et al., 2017b). Counting was thus done on one section selected from the region where the anterior commissure was apparent A8.2 (Kuenzel and Masson, 1988). The counting area was positioned beneath the anterior commissure (Fig. 2A). This region was not initially analyzed because, due to damage occurring during the separations of hemispheres, counting of POA was not feasible in few individuals and in some individuals the area was available only in one of the two brain hemispheres. However, given the involvement of this area in the motion perception of a living conspecific evidenced by our previous study (Mayer et al., 2017b), we decided that it was of interest to investigate it all the same. Thus, POA data for either one or both hemispheres were available overall for 19 subjects (10 experimental and nine controls). Specifically, data for the left hemisphere were available for 10 experimental and six control animals, whereas for the right hemisphere for seven experimental and six control animals. For the overall estimation of the neuronal activity in the POA the measurements from two hemispheres, if available, were averaged, otherwise the estimation was based on the measurement from the only hemisphere available. The cell densities were standardized to 1 mm^2.

Behavioral analysis

The video recordings of the behavioral procedure were analyzed off-line. For every animal, we measured the latency of the first approach to the stimulus (seconds)

and the ratio of time spent near the stimulus (i.e., above the platform adjacent to the screen) over six minutes. This was calculated by the following formula: number of seconds spent near the stimulus/360 s. Mathematically the values obtained by this formula can range from 0 to 1. High values of the ratio indicate a higher proportion of test time spent near the stimulus, and vice versa for low values. Moreover, the frequency of different behaviors was quantified every 10 sec for the entire 6-min period. The behaviors measured were indexes of motor activity, vocalizations and head orientations. Motoric activity indexes scored were walking and pecking. Different types of vocalizations measured were soft calls, distress calls and contact calls. Head orientation was measured with respect to the stimulus and could range from 0° to 315° with 45° as unit. At 0° the beak was oriented straight to the stimulus whereas, at 180° the beak was directed toward the black opposite screen. Head orientation 0° was interpreted as binocular episode, whereas, head orientations 45°, 90°, 270° and 315° were scored as monocular episodes (45° and 90° represented left monocular episodes, whereas 270° and 315° were right monocular episodes). A binocularity index was computed for each subject as follows: binocular episodes' frequency/(binocular episodes' frequency + monocular episodes' frequency). Moreover, an eye lateralization index was computed for each subject as follows: right monocular episodes/(right monocular episodes + left monocular episodes). Scores of both indexes ranged from 1 (e.g., for the eye-lateralization index this value was obtained if only the right eye was used for monocular episodes), to 0 (only the left eye was used). Being computed this way, the values of the eye lateralization index were directly comparable with the brain lateralization index (see above). Because of a complete decussation of the optic fiber in birds (Walls, 1942), each eye projects mainly to the contralateral brain hemisphere making it particularly interesting to investigate the relationship between eye use and lateralized brain activity.

Statistical analysis

The presence of a difference in the density of c-Fos-ir cells in IMM, septum and arcopallium was tested by a repeated measurement ANOVA, with a between-subject factor ''group'' (2 levels: experimental and control) and two within-subject factors: ''area'' (3 levels: septum, IMM and arcopallium) and ''hemisphere'' (2 levels: left and right). For post-hoc analyses of the differences between the groups, two-tailed t-tests were performed for each brain area. The lateralization within the groups was tested by a two-tailed paired t-test. To test lateralization differences between the groups, independent samples two-tailed t-tests were performed for each lateralization index. No Bonferroni correction was applied on the t-tests, since our experimental design was based on strong a priori expectations on the pattern of activation to be found in the various areas (Fay and Gerow, 2013), derived from our previous studies (Mayer et al., 2016b; Mayer et al., 2017a,b). After the completion of the statistical analysis of the other three brain areas, the densities of c-Fos-ir cells in the POA were estimated as additional, independent post hoc and compared between the groups with a two-tailed t-test. Lateralization was not tested and measurements were pooled between the two hemispheres (see above).

Each behavior was compared between the two groups with a two-tailed t-test for independent samples. The binocular index and the eye lateralization indexes were compared between the two groups with an independent samples two-tailed t-test. The eye lateralization index was compared also to chance level (0.5) for the two groups separately with a one-sample two-tailed t-test. In order to verify whether behavioral differences could account for the differences in c-Fos-ir cells densities, correlations between each behavior and each brain area were tested with Pearson's correlation analysis. Finally, Pearson's correlation analysis was run also to test correlations between eye preference (eye lateralization index) and brain lateralization. All statistical analyses were performed with the software IBM SPSS Statistics (v. 20).

RESULTS

Behavior

Overall, no significant differences were present between the two groups for any of the behavioral measurements. The approach latency to the stimulus was 121.92 ± 23.405 in the experimental group and 157.58 ± 26.743 in the control group ($t_{(22} = -1.004$, $p = 0.326$), the ratio of time spent near the stimulus was 0.661 ± 0.0649 in the experimental and 0.523 ± 0.072 in the control ($t_{(22)} = 1.434$, $p = 0.166$). Also the motoric activities were not different between the two groups (walking: experimental 7.25 ± 0.986, control 7.42 ± 1.317, $t_{(22)} = -0.101$, $p = 0.920$; pecking: experimental 7.83 ± 1.272, control 6 ± 1.255, $t_{(22)} = 1.026$, $p = 0.316$). In both groups several call types were emitted with similar frequencies (soft calls: experimental 15.75 ± 1.793, control 12.58 ± 1.479, $t_{(22)} = 1.362$, $p = 0.187$; distress calls: experimental 1.75 ± 1.067, control 3.08 ± 1.221, $t_{(22)} = -0.822$, $p = 0.420$; contact calls: experimental 3.92 ± 0.753, control 5.58 ± 0.949, $t_{(22)} = -1.375$, $p = 0.183$). Furthermore, no eye preference for looking at the stimuli was detectable in any of the two groups. In both groups the eye lateralization index was not different from chance level (0.5), in the experimental group it was 0.515 ± 0.0428 ($t_{(11)} = 0.349$, $p = 0.734$) and in the control group it was 0.453 ± 0.056 ($t_{(11)} = -0.845$, $p = 0.416$). Consistent with this, the eye lateralization index was not different between the two groups ($t_{(22)} = 0.883$, $p = 0.387$) and also the binocular index did not show any differences between the two groups (experimental 0.2557 ± 0.025, control 0.224 ± 0.013 $t_{(22)} = 1.123$, $p = 0.274$).

c-Fos-immunoreactive cell counting

All 12 brains from the experimental and 12 brains from the control group were successfully stained for c-Fos. Due to

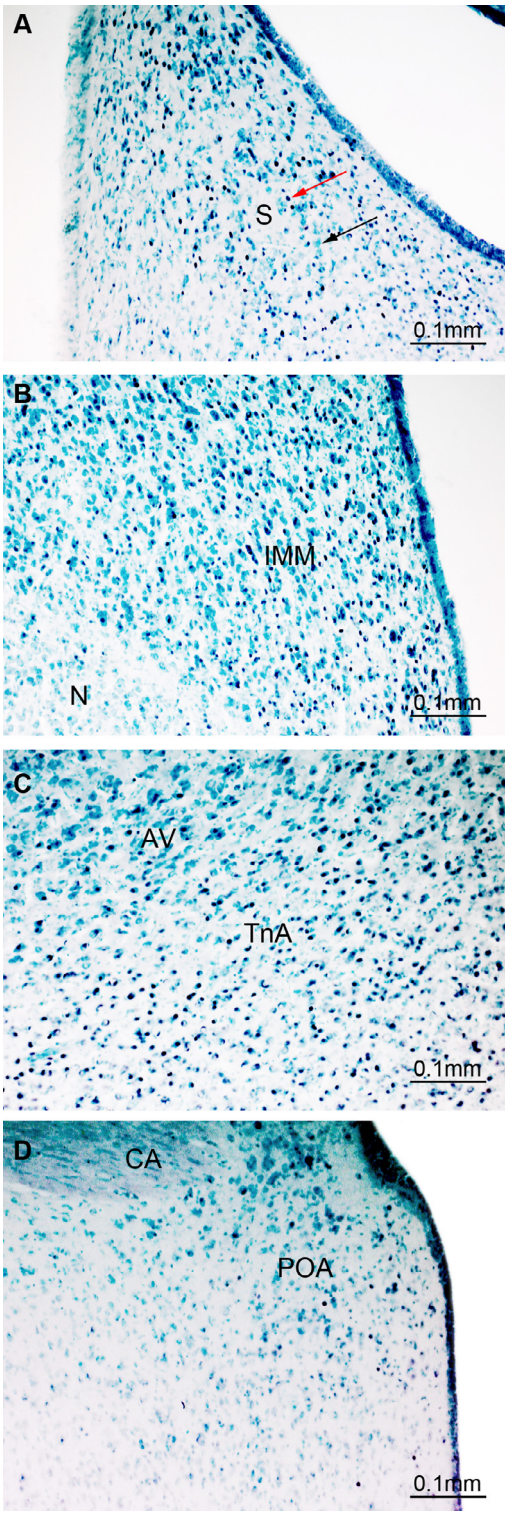

Fig. 3. c-Fos staining. Photomicrographs of coronal sections of experimental chicks' brains. c-Fos-ir cell nuclei are stained black (red arrow) and are easily discernible from the methyl-green counter-stained cells (black arrow). (A) High number of c-Fos-ir nuclei in the dorsal septum. (B) High number of c-Fos-ir nuclei in IMM. (C) c-Fos-ir nuclei within arcopallium. (D) c-Fos-ir cells in the POA. S – Septum, IMM – intermediate medial mesopallium, N – nidopallium, AV – ventral arcopallium, TnA – nucleus taeniae, POA – preoptic area, CA – anterior commissure. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

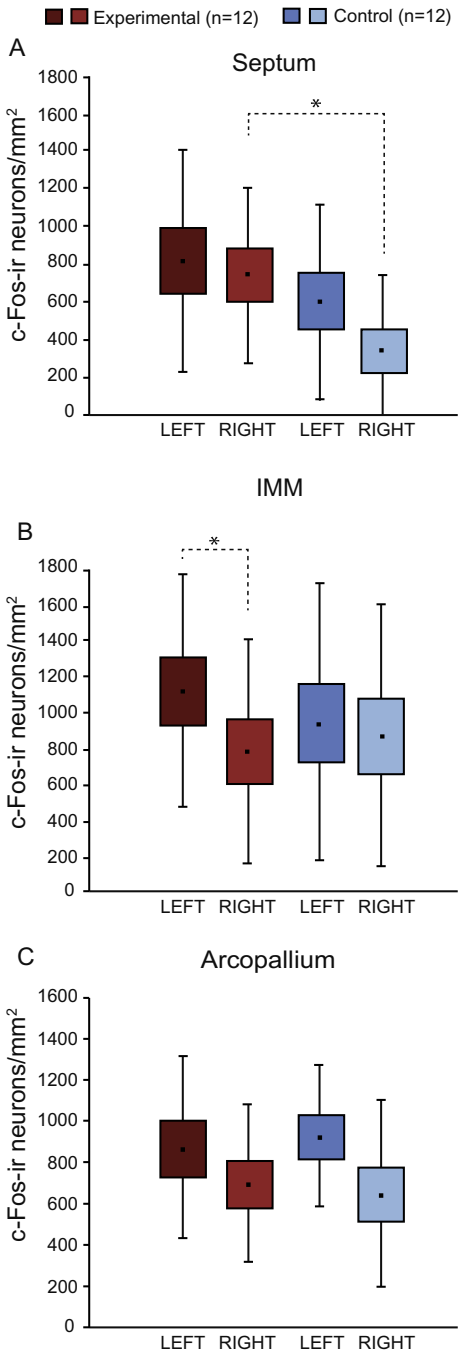

Fig. 4. Estimated densities. Measured c-Fos-ir cellular densities in the two groups of chicks. (A) Significantly higher number of c-Fos-ir cells in the right septum of experimental chicks compared to controls. (B) A high number of c-Fos-ir cells in the left than in the right IMM of the experimental chicks. (C) No difference between groups was present in the arcopallium. Graph-plot: mean (black square), s.e.m. (box) and s.d (whisker). (*Indicates $p < 0.05$). Densities of c-Fos-ir cells per mm^2 are represented on the Y-axis.

the methyl-green counterstaining nuclei of all neurons were stained green, whereas the nuclei of c-Fos-ir cells were stained black after the immunohistochemical procedure and background staining was minimal. Thus, c-Fos-ir cells could be easily discerned from other neurons (Fig. 3). All birds showed individual distributions

of c-Fos-ir cells within the measured areas and the two hemispheres. As already mentioned in the methods, not all the subjects provided an intact POA. In some individuals, this area was damaged and not analysable in at least one hemisphere. However, if the area was intact, the labeled cells were easily distinguishable from the background.

The repeated measurement ANOVA on septum, IMM and arcopallium revealed significant main effect of area ($F_{(2,44)} = 7.528$, $p = 0.002$) and hemisphere ($F_{(1,22)} = 4.595$, $p = 0.043$). Moreover a significant interaction of area x hemisphere x group ($F_{(2,44)} = 3.800$, $p = 0.030$), revealed significant differences in densities of c-Fos-ir cells between the experimental and control group in a brain region and hemisphere-dependent fashion. Statistical post hoc analysis for the three areas is reported below. The number of c-Fos-ir cells differed considerably in the right septum between the experimental and the control group ($t_{(22)} = 2.242$, $p = 0.035$; Fig. 4A). Experimental birds showed more than twice as much c-Fos-ir cells within the right septum (742.9 ± 135.4 cells/mm^2) compared to the controls (343.8 ± 115.6 cells/mm^2). Such significant difference between the two groups was not present in the left septum (experimental: 818.4 ± 172 cells/mm^2, control: 604.4 ± 149.9 cells/mm^2; $t_{(22)} = 0.938$, $p = 0.359$). Differences between the two groups were also not present in the left IMM (experimental: 1123.9 ± 189.4 cells/mm^2, control: 952.5 ± 222.9 cells/mm^2; $t_{(22)} = 0.586$, $p = 0.564$; Fig. 4B) nor in the right IMM (experimental: 785.8 ± 179 cells/mm^2, control: 876.9 ± 210.9 cells/mm^2; $t_{(22)} = -0.330$, $p = 0.745$). Also the arcopallium did not show any difference between the two groups (experimental left: 869.8 ± 129.4 cells/mm^2, control left: 926.2 ± 101.5 cells/mm^2; $t_{(22)} = -0.343$, $p = 0.735$; experimental right: 697.8 ± 112.4 cells/mm^2, control right: 645.6 ± 132.4 cells/mm^2; $t_{(22)} = 0.301$, $p = 0.766$; Fig. 4C). Overall, a left lateralization trend was visible in all measured brain areas of both groups (see Fig. 4). To examine the presence of significant lateralization we performed within-group comparisons of brain regions of the left hemisphere with the corresponding brain regions of the right hemisphere. In the experimental group we found a significant lateralization only in the IMM ($t_{(11)} = 2.809$, $p = 0.017$), whereas the differences were not significant in septum ($t_{(11)} = 0.658$, $p = 0.524$) nor in the arcopallium ($t_{(11)} = 1.626$, $p = 0.132$). The lateralization of the control group was not significant in any of the brain areas (IMM, $t_{(11)} = 0.349$, $p = 0.734$; septum: $t_{(11)} = 1.817$, $p = 0.096$; arcopallium: $t_{(11)} = 1.653$, $p = 0.126$).

Counting of the POA revealed higher c-Fos-ir density in the experimental group compared to the control: experimental birds showed more than twice as much c-Fos-ir cells compared to the controls (experimental $n = 10$: 473.3 ± 104.7 cells/mm^2, control $n = 9$: 216.3 ± 53.9 cells/mm^2; $t_{(17)} = 2.1090$, $p = 0.050$; see Fig. 5).

Correlations of neuronal activity with behavior

We performed correlation analyses between measured brain activities and behavioral parameters without distinguishing between groups, since we did not observe relevant differences between the groups in this respect. We found two significant correlations on two related behaviors, which we report here below, because it might be informative for future studies. Pearson's correlation test revealed a significant positive correlation between latency to approach the stimulus and density of c-Fos-ir cells in the left arcopallium ($r = 0.505$, $n = 24$, $p = 0.012$) and a significant negative correlation between the ratio of time spent near the stimulus and c-Fos-ir cellular density in the left arcopallium ($r = -0.465$, $n = 24$, $p = 0.022$) (see Fig. 6). These correlations were not significant for the right hemisphere (latency: $r = -0.243$, $n = 24$, $p = 0.253$; ratio: $r = 0.162$, $n = 24$, $p = 0.451$). Noteworthy, the latency to approach a stimulus and the ratio of time spent near it are two inversely proportional measures of the preference for the stimulus. In fact, in the current test a

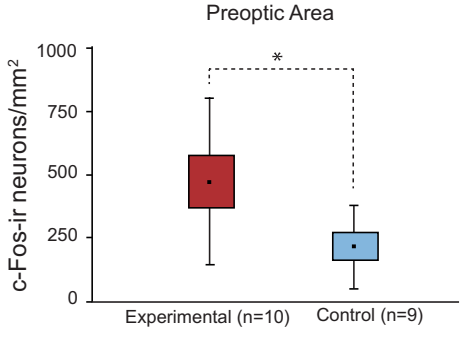

Fig. 5. Preoptic area. Measured c-Fos-ir cellular densities in the preoptic area, showing a significantly higher number of c-Fos-ir cells in the experimental chicks compared to the control chicks. Graph-plot: mean (black square), s.e.m. (box) and s.d (whisker). (*Indicates $p < 0.05$). Densities of c-Fos-ir cells per mm^2 are represented on the Y-axis.

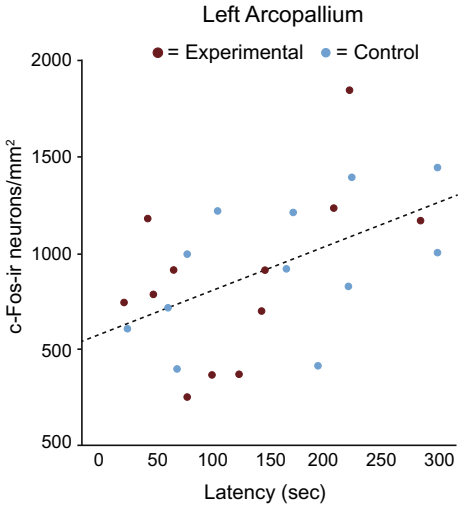

Fig. 6. Brain-behavior correlation. Scatterplot showing the positive correlation between the latency to first approach the stimulus (X-axis) and the number of c-Fos ir cells within left arcopallium (Y-axis).

lower latency to approach one stimulus was usually associated with a higher time spent close to it during the test.

DISCUSSION

The current study is the last of a series of three separate experiments demonstrating septal activation in response to the movement of alive conspecifics, and the second experiment to reveal activation of the preoptic area (Mayer et al., 2017a,b). In the present study, septal activity in the right hemisphere was higher after exposure to the predisposed speed-change stimulus, compared to chicks exposed to the control speed-constant stimulus. Moreover, also in the POA we found a higher number of c-Fos-ir cells for chicks exposed to the speed-change stimulus, compared to the control group. The observed differences were region specific and not due to the overall activity of the brains, since the densities of c-Fos-ir cells in the arcopallium and IMM were not different between the groups. In addition, the differential activation of the septal nuclei and of the preoptic region can be explained only by the visual stimulation provided by the experimental stimuli: both groups of chicks were exposed to the same visual environment, and no behavioral differences could be observed between them. This was probably facilitated by the fact that both the test stimuli present various features that are socially attractive to chicks: movement itself, the red color, the appropriate shape and size to elicit optimal filial imprinting (see Rosa-Salva et al., 2016 for a discussion). It should also be noted that the procedure employed in this experiment was specifically designed not to cause behavioral differences between the two groups, which could potentially complicate the interpretation of the brain results. In fact, the preference for the speed-change stimulus had already been established in our own previous behavioral study (Rosa-Salva et al., 2016). Since we obtained our measurements from chicks exposed only to either one of the two stimuli, rather than from chicks that showed different preferences between the two, the focus of the investigation was not on the brain structures involved in the expression of the choice, but on those involved in the processing and response to the predisposed and non-predisposed stimuli.

We thus demonstrated selective responsiveness to this preferred motion pattern that also elicits animacy perception in human observers (Tremoulet and Feldman, 2000). This adds to the recent evidence that nodes of the social behavior network (Newman, 1999; O'Connell and Hofmann, 2011; Goodson and Kingsbury, 2013) might be already involved in early social responses of naïve animals exposed for the first time to an alive conspecific (Mayer et al., 2017a,b).

The difference in septal and POA activation could be associated with the different social responses elicited by the motion of the two stimuli. We assume that the exposure to the speed-change stimulus had a social valence for the experimental subjects, which are compelled to look for an imprinting object at this stage of development (Bateson, 1966). The test exposure represented chicks' first encounter with a salient visual object, whose appearance is optimal to elicit imprinting. Also, our task was based on a social affiliative response (filial approach). Moreover, the same pattern of activation was found in chicks exposed to an unquestionably social stimulus, a living conspecific (Mayer et al., 2017a,b). Finally, this is also consistent with the widespread involvement of these two brain areas in social functions (Goodson, 1998; Liu et al., 2001; Taziaux et al., 2006; Nishizawa et al., 2011; Klatt and Goodson, 2013). Septum and POA could also be involved in establishing the emotional valence of the stimulus, as suggested by the fact that septum belongs to the mesolimbic reward system that process the valence of external stimuli (O'Connell and Hofmann, 2011).

Social predispositions are believed to be adaptive in that they direct subsequent filial imprinting toward appropriate objects, prioritizing attention toward animate creatures (Rosa-Salva et al., 2015). It is unknown so far, if septum or POA are involved in the learning process of filial imprinting, since no research has been conducted on the role of these structures in early social development. However, their role in pair bonding and parental care is well established in adult mammals and birds (Liu et al., 2001; Balthazart and Ball, 2007; Goodson et al., 2009). Those social behaviors are mediated by the neuropeptides arginine vasopressin and oxytocin in mammals (Liu et al., 2001; Lim and Young, 2006; Carter et al., 2008; Leng et al., 2008) and by their homologs arginine vasotocin and mesotocin in birds (Baeyens and Cornett, 2006; Goodson et al., 2009; Klatt and Goodson, 2013), for which these areas are rich of receptors (Newman, 1999; Panzica et al., 2002; O'Connell and Hofmann, 2011; Goodson and Kingsbury, 2013). Also, the anatomical location where we counted inside POA (medial preoptic area) is dense of aromatase expressing cells, a signature of testosterone action in the brain (Balthazart and Ball, 2007). Interestingly, the levels of testosterone in the IMM are associated with the preference for predisposed stimuli in chicks (Bolhuis et al., 1986). Therefore, the presence of sex steroid hormonal receptors within septum and POA may also suggest their involvement in imprinting on predisposed stimuli. Future studies could investigate which kind of hormonal receptors are expressed in septal and preoptic neurons activated by the predisposed stimulus and whether the learning process of filial imprinting modulates septal and POA activity differently in relation to the presence of predisposed features in the imprinting stimulus.

Since the activity difference in septum was caused by exposure to visual cues of animacy, another question arises: what is the source of visual or visually modulated information that influences septal activity? So far there is no evidence that septum is directly devoted to visual processing. Visual input to septum could reach septum through its interconnection with the hippocampus (Atoji et al., 2002; Montagnese et al., 2004, 2008; Atoji and Wild, 2004), which receives visual information from the visual Wulst (see Atoji and Wild, 2006). This is the telencephalic terminal of the thalamofugal visual projection and is considered the avian homolog of the primary visual cortex (Medina and Reiner, 2000; Wild and Williams, 2000).

This is also compatible with a possible role of septum in modulating the imprinting process, since both visual Wulst and hippocampus have been implicated in imprinting (Güntürkün et al., 1993; Sadananda and Bischof, 2004; Maekawa et al., 2007; Aoki et al., 2015).

It is still unclear which might be the specific functional consequences of the activation of septum and preoptic area in this context. However, we can propose some speculations based on the fact that c-Fos acts on several late response genes involved in modulation of connectivity (Sheng and Greenberg, 1990). The activity we measured could be related to rewiring in the brain areas of interest, reflecting processes associated with the tuning of the network of areas that control social responses, such as filial approach, toward the most appropriate social objects. The plastic changes might reflect the adjustment associated with the first coming online of some components of the social-decision-making network, concurrently with the first socially relevant experience of the naïve animals.

The tractus septopallio-mesencephalicus, which runs through septum in the dorso-ventral direction, connects the visual Wulst back to the optic tectum (Karten et al., 1973; Reiner and Karten, 1983; Manns et al., 2007). The optic tectum is an important structure for orienting toward stimuli (Jarvis, 1974; Hodos and Karten, 1974) and for the perception of motion (Frost and Nakayama, 1983; Frost et al., 1988, 1990), with some tectal neurons of domestic chicks responding specifically to changes in speed (Verhaal and Luksch, 2015). An involvement of the optic tectum in social predispositions was also postulated (Rosa-Salva et al., 2015). However, the tractus septopallio-mesencephalicus has never been shown to terminate in septum and thus it is unclear if it can contribute to the septal activation.

Finally, it is important to consider that subtelencephalic regions might play important role in innate complex stimulus recognition in chicks (Zachar et al., 2008; Rosa-Salva et al., 2015) and some of them, such as the pretectal nucleus, sends projections to the septum (Montagnese et al., 2008). Thus, it is also possible to hypothesize a contribution of subtelencephalic regions to the septal activation found in the present study.

We also considered which visual features caused the observed effects. The two stimuli were balanced for most low-level features, such as color, size, distance traveled and average speed. However, they necessarily differed in the maximum speed reached by each object. In principle, we cannot exclude that the differences observed in this study depend on this factor, but we consider this to be highly unlikely. Our previous behavioral study clearly demonstrated that chicks' social preference for the speed-change stimulus is elicited by the presence of visible speed changes, and not by speed itself (Rosa-Salva et al., 2016): occluding the moments of speed change abolished the preference. Given the involvement of septum and preoptic area in social behaviors, it is reasonable to assume that the activation of these areas is driven by the same visual cues that affect chicks' affiliative responses. Moreover, identical patterns of activation in the right septum and in the preoptic area have been found in our previous studies (Mayer et al., 2017a,b). Notably, in these studies chicks were exposed to a clearly social dynamic stimulus (a living conspecific), which obviously differs markedly from the speed-change stimulus in its low-level perceptual features, including its speed of motion.

Another interesting aspect of our results is that the effect found in septum was restricted to the right hemisphere. Higher right hemisphere activation has been reported for human adults (Grossman et al., 2000) and infants (Ichikawa et al., 2010) viewing point-light displays of biological motion, another kind of stimuli associated with animacy perception that elicit social predisposition in chicks (Vallortigara et al., 2005). Likewise, in chicks the left eye-system (right hemisphere) is preferentially used to monitor this kind of stimuli (Rugani et al., 2015). Overall, this is in line with the preferential involvement of the right hemisphere in social responses, social recognition and the rapid recognition of emotional stimuli (Rogers et al., 2013; Vallortigara and Versace, 2017). In chicks the left eye system is more reactive to emotionally charged stimuli (Rogers and Anson, 1979), is dominant for cognitive abilities involved in the formation of the dominance hierarchies (Daisley et al., 2010), is involved in early testosterone-induced courtship behavior (Rogers et al., 1985), individual recognition of social companions and social learning by observation (Vallortigara and Andrew, 1991; Vallortigara, 1992; Vallortigara et al., 2001; Deng and Rogers, 2002; Rosa-Salva et al., 2009, 2012b).

To understand the lateralized effect observed in septum, it is important to consider the overall lateralization pattern that emerged from our results. Regardless of the experimental condition, all brain areas showed a trend for higher activity in the left hemisphere compared to the right one: this may represent a baseline lateralization effect, independently from the experimental stimuli. A similar trend for a spontaneous higher activation of the left hemisphere has been reported in our previous study on septal activation in chicks exposed to a living conspecific. Also in this case, the effect observed in septum was limited to the right hemisphere, resulting in a similar level of activation of the left and right septum in chicks exposed to the conspecific, while the septum of the control group showed the usual spontaneous left lateralization, as did other areas whose activation was not different between the groups (Mayer et al., 2017b). Activation in the right septum could be more easily modulated by exposure to visual cues typical of social stimuli than in the left septum, due to the masking effect caused by the left hemisphere's spontaneous higher level of activity (e.g., a ceiling effect).

It is unclear why this general trend for left lateralization was significant only in the IMM of chicks exposed to the speed-change stimulus, even though the same trend was visible also in the control group. This could be associated with the fact that biochemical and morphological changes associated with imprinting are generally more marked in the left IMM (Horn, 2004), which might enhance the general leftward trend especially for those chicks exposed to the preferred stimulus (a more attractive imprinting object). However, lateralization

in imprinting learning is more complex than that, with interactions between the different types of information to be stored and the time course of memory formation (e.g. Vallortigara and Andrew, 1994; Solomonia et al., 1997, 1998; Andrew, 1999; Mayer et al., 2016b).

The same general trend for left lateralization was present in arcopallium for both groups. Moreover, left arcopallium activity correlated positively with latency of first approach. Since arcopallium is involved in fear responses (Phillips, 1968; Martin et al., 1979), this could reflect individual variation in the level of cautiousness: latency to approach the stimulus will be influenced by the duration of the initial freezing response in the novel environment. However, usually the control of fear responses is lateralized in favor of the right arcopallium (Phillips and Youngren, 1986; see also Rosa-Salva et al., 2007). Here the correlation regarded the activation of arcopallium of the left hemisphere, making an interpretation in terms of simple fear responses less straightforward. A more plausible interpretation involves the left hemisphere specialization for response control mechanisms (Bullock and Rogers, 1986; McKenzie and Andrew, 1996; Andrew, 2009): e.g., the left hemisphere is especially involved in deciding whether to approach a potential imprinting object (McKenzie et al., 1998). We hypothesize that the more reluctant a subject was of moving in the environment, the more the left hemisphere was activated by the task of controlling (inhibiting) the emission of the approach response.

Overall, the results of the present paper demonstrate an involvement of right septal nuclei and preoptic area in early social responses of visually naïve animals, in line with previous studies showing that they are activated by the first exposure to a living conspecific (Mayer et al., 2017a,b). This confirms that these important nodes of the social behavior network are already engaged in social responses at birth and that learning experiences associated with social companions are not needed for their involvement in this function. Moreover, we also demonstrated for the first time a sensitivity of these brain areas to the very same elementary motion cues that are typical of animate creatures and elicit chicks' social predispositions for filial approach (Rosa-Salva et al., 2016), human infants' preferential attention (Frankenhuis et al., 2013) and adults' perception of animacy (Tremoulet and Feldman, 2000).

COMPLIANCE WITH ETHICAL STANDARDS

All applicable, European and Italian guidelines for the care and use of animals were followed. All procedures performed were in accordance with the ethical standards of the University of Trento, where the study was conduct. Study has been approved by the research ethics committee of the University of Trento and by the Italian Ministry of Health (permit number 20269/A).

Acknowledgments—Funding: This work was supported by a grant from the European Research Council under the European Union's Seventh Framework Programme (FP7/2007-2013)/ Advanced Grant ERC PREMESOR G.A. [n° 295517] to Giorgio Vallortigara.

REFERENCES

Akerman B, Anderson B, Fabricius E, Svensson L (1960) Observations on central regulation of body temperature and of food and water intake in the pigeon (Columba livia). Acta Physiol Scand 50:328–336. http://dx.doi.org/10.1111/j.1748-1716.1960.tb00187.x.

Albert DJ, Chew GL (1980) The septal forebrain and the inhibitory modulation of attack and defense in the rat. A review. Behav Neural Biol 30:357–388. http://dx.doi.org/10.1016/S0163-1047(80)91247-9.

Ambalavanar R, Van der Zee EA, Bolhuis JJ, McCabe BJ, Horn G (1993) Co-expression of Fos immunoreactivity in protein kinase (PKCγ)-positive neurones: quantitative analysis of a brain region involved in learning. Brain Res 606:315–318. http://dx.doi.org/10.1016/0006-8993(93)91000-I.

Andrew RJ (1999) The differential roles of right and left sides of the brain in memory formation. Behav Brain Res 98:289–295. http://dx.doi.org/10.1016/S0166-4328(98)00095-3.

Andrew RJ (2009) Origins of asymmetry in the CNS. Semin Cell Dev Biol 20:485–490. http://dx.doi.org/10.1016/j.semcdb.2008.11.001.

Aoki N, Yamaguchi S, Kitajima T, Takehara A, Katagiri-Nakagawa S, Matsui R, Matsushima T, Homma KJ (2015) Critical role of the neural pathway from the intermediate medial mesopallium to the intermediate hyperpallium apicale in filial imprinting of domestic chicks (Gallus gallus domesticus). Neuroscience 308:115–124. http://dx.doi.org/10.1016/j.neuroscience.2015.09.014.

Atoji Y, Wild JM (2004) Fiber connections of the hippocampal formation and septum and subdivisions of the hippocampal formation in the pigeon as revealed by tract tracing and kainic acid lesions. J Comp Neurol 475:426–461. http://dx.doi.org/10.1002/cne.20186.

Atoji Y, Wild JM (2006) Anatomy of the avian hippocampal formation. Rev Neurosci 17:3–16. http://dx.doi.org/10.1515/revneuro.2006.17.1-2.3.

Atoji Y, Wild JM, Yamamoto Y, Suzuki Y (2002) Intratelencephalic connections of the hippocampus in pigeons (Columba livia). J Comp Neurol 447:177–199. http://dx.doi.org/10.1002/cne.10239.

Baeyens DA, Cornett LE (2006) The cloned avian neurohypophysial hormone receptors. Comp Biochem Physiol B Biochem Mol Biol 143:12–19. http://dx.doi.org/10.1016/j.cbpb.2005.09.012.

Balthazart J, Absil P, Gérard M, Appeltants D, Ball GF (1998a) Appetitive and consummatory male sexual behavior in Japanese quail are differentially regulated by subregions of the preoptic medial nucleus. J Neurosci 18:6512–6527.

Balthazart J, Ball GF (2007) Topography in the preoptic region: Differential regulation of appetitive and consummatory male sexual behaviors. Front Neuroendocrinol 28:161–178. http://dx.doi.org/10.1016/j.yfrne.2007.05.003.

Balthazart J, Evrard L, Surlemont C (1990) Effects of the nonsteroidal inhibitor R76713 on testosterone-induced sexual behavior in the Japanese quail (Coturnix coturnix japonica). Horm Behav 24:510–531.

Balthazart J, Foidart A, Houbart M, Prins GS, Ball GF (1998b) Distribution of androgen receptor-immunoreactive cells in the quail forebrain and their relationship with aromatase immunoreactivity. J Neurobiol 35:323–340.

Bateson PPG (1966) The characteristics and context of imprinting. Biol Rev 41:177–217. http://dx.doi.org/10.1111/j.1469-185X.1966.tb01489.x.

Bharati IS, Goodson JL (2006) Fos responses of dopamine neurons to sociosexual stimuli in male zebra finches. Neuroscience 143:661–670. http://dx.doi.org/10.1016/j.neuroscience.2006.08.046.

Bolhuis JJ (1991) Mechanisms of avian imprinting: a review. Biol Rev 66:303–345. http://dx.doi.org/10.1111/j.1469-185X.1991.tb01145.x.

Bolhuis JJ, McCabe BJ, Horn G (1986) Androgens and imprinting: Differential effects of testosterone on filial preference in the

domestic chick. Behav Neurosci 100:51–56. http://dx.doi.org/10.1037/0735-7044.100.1.51.
Bullock SP, Rogers LJ (1986) Glutamate-induced asymmetry in the sexual and aggressive behavior of young chickens. Pharmacol Biochem Behav 24:549–554. http://dx.doi.org/10.1016/0091-3057(86)90556-3.
Butler AB, Reiner A, Karten HJ (2011) Evolution of the amniote pallium and the origins of mammalian neocortex. Ann N Y Acad Sci 1225:14–27. http://dx.doi.org/10.1111/j.1749-6632.2011.06006.x.
Carter CS, Grippo AJ, Pournajafi-Nazarloo H, Ruscio MG, Porges SW (2008), Oxytocin, vasopressin and sociality. In: Landgraf IDN and R (ed) Progress in Brain Research. Elsevier, pp 331–336.
Cheng M-F, Chaiken M, Zuo M, Miller H (1999) Nucleus taenia of the amygdala of birds: anatomical and functional studies in ring doves (streptopelia risoria) and european starlings (sturnus vulgaris). Brain Behav Evol 53:243–270. http://dx.doi.org/10.1159/000006597.
Choi GB, Dong H, Murphy AJ, Valenzuela DM, Yancopoulos GD, Swanson LW, Anderson DJ (2005) Lhx6 delineates a pathway mediating innate reproductive behaviors from the amygdala to the hypothalamus. Neuron 46:647–660. http://dx.doi.org/10.1016/j.neuron.2005.04.011.
Daisley JN, Vallortigara G, Regolin L (2010) Logic in an asymmetrical (social) brain: Transitive inference in the young domestic chick. Soc Neurosci 5:309–319. http://dx.doi.org/10.1080/17470910903529795.
Deng C, Rogers LJ (2002) Social recognition and approach in the chick: lateralization and effect of visual experience. Anim Behav 63:697–706. http://dx.doi.org/10.1006/anbe.2001.1942.
Di Giorgio E, Frasnelli E, Rosa-Salva O, Scattoni ML, Puopolo M, Tosoni D, NIDA-Network, Simion F, Vallortigara G (2016b) Difference in visual social predispositions between newborns at low- and high-risk for autism. Sci Rep. http://dx.doi.org/10.1038/srep26395.
Di Giorgio E, Loveland JL, Mayer U, Rosa-Salva O, Versace E, Vallortigara G (2016a) Filial responses as predisposed and learned preferences: Early attachment in chicks and babies. Behav Brain Res. http://dx.doi.org/10.1016/j.bbr.2016.09.018.
Di Giorgio E, Lunghi M, Simion F, Vallortigara G (2016c) Visual cues of motion that trigger animacy perception at birth: the case of self-propulsion. Dev Sci. http://dx.doi.org/10.1111/desc.12394.
Fay DS, Gerow K (2013), A biologist's guide to statistical thinking and analysis. WormBook, ed. The C. elegans Research Community, doi/10.1895/wormbook.1.159.1.
Ferris CF, Gold L, De Vries GJ, Potegal M (1990) Evidence for a functional and anatomical relationship between the lateral septum and the hypothalamus in the control of flank marking behavior in golden hamsters. J Comp Neurol 293:476–485. http://dx.doi.org/10.1002/cne.902930310.
Frankenhuis WE, House B, Barrett HC, Johnson SP (2013) Infants' perception of chasing. Cognition 126:224–233.
Frost BJ, Cavanagh P, Morgan B (1988) Deep tectal cells in pigeons respond to kinematograms. J Comp Physiol A 162:639–647. http://dx.doi.org/10.1007/BF01342639.
Frost BJ, Nakayama K (1983) Single visual neurons code opposing motion independent of direction. Science 220:744–745.
Frost BJ, Wylie DR, Wang Y-C (1990) The processing of object and self-motion in the tectofugal and accessory optic pathways of birds. Vision Res 30:1677–1688. http://dx.doi.org/10.1016/0042-6989(90)90152-B.
Gahr M (2001) Distribution of sex steroid hormone receptors in the avian brain: functional implications for neural sex differences and sexual behaviors. Microsc Res Tech 55:1–11. http://dx.doi.org/10.1002/jemt.1151.
Goodson JL (2005) The vertebrate social behavior network: evolutionary themes and variations. Horm Behav 48:11–22. http://dx.doi.org/10.1016/j.yhbeh.2005.02.003.
Goodson JL (1998) Territorial aggression and dawn song are modulated by septal vasotocin and vasoactive intestinal polypeptide in male field sparrows (spizella pusilla). Horm Behav 34:67–77. http://dx.doi.org/10.1006/hbeh.1998.1467.
Goodson JL, Kingsbury MA (2013) What's in a name? Considerations of homologies and nomenclature for vertebrate social behavior networks. Horm Behav 64:103–112. http://dx.doi.org/10.1016/j.yhbeh.2013.05.006.
Goodson JL, Schrock SE, Klatt JD, Kabelik D, Kingsbury MA (2009) Mesotocin and nonapeptide receptors promote estrildid flocking behavior. Science 325:862–866. http://dx.doi.org/10.1126/science.1174929.
Grossman E, Donnelly M, Price R, Pickens D, Morgan V, Neighbor G, Blake R (2000) Brain areas involved in perception of biological motion. J Cogn Neurosci 12:711–720. http://dx.doi.org/10.1162/089892900562417.
Güntürkün O, Miceli D, Watanabe M (1993) Anatomy of the avian thalamofugal pathway. In: Vision, brain and behavior in birds. London: The MIT Press.
Guzowski JF, Timlin JA, Roysam B, McNaughton BL, Worely PF, Barnes CA (2005) Mapping behaviorally relevant neural circuits with immediate-early gene expression. Curr Opin Neurobiol 15:599–606. http://dx.doi.org/10.1016/j.conb.2005.08.018.
Hamm AO, Weike AI (2005) The neuropsychology of fear learning and fear regulation. Int J Psychophysiol 57:5–14. http://dx.doi.org/10.1016/j.ijpsycho.2005.01.006.
Hanics J, Teleki G, Alpár A, Székely AD, Csillag A (2017) Multiple amygdaloid divisions of arcopallium send convergent projections to the nucleus accumbens and neighboring subpallial amygdala regions in the domestic chicken: a selective pathway tracing and reconstruction study. Brain Struct Funct 222(1):301–315.
Hodos W, Karten HJ (1974) Visual intensity pattern discrimination deficits after lesions of the optic lobe in pigeons. Brain Behav Evol 9:165–194.
Horn G (1979) Imprinting – In search of neural mechanisms. Trends Neurosci 2:219–222. http://dx.doi.org/10.1016/0166-2236(79)90086-9.
Horn G (1998) Visual imprinting and the neural mechanisms of recognition memory. Trends Neurosci 21:300–305. http://dx.doi.org/10.1016/S0166-2236(97)01219-8.
Horn G (2004) Pathways of the past: the imprint of memory. Nat Rev Neurosci 5:108–120. http://dx.doi.org/10.1038/nrn1324.
Horn G, McCabe BJ (1984) Predispositions and preferences. Effects on imprinting of lesions to the chick brain. Anim Behav 32:288–292. http://dx.doi.org/10.1016/S0003-3472(84)80349-8.
Ichikawa H, Kanazawa S, Yamaguchi MK, Kakigi R (2010) Infant brain activity while viewing facial movement of point-light displays as measured by near-infrared spectroscopy (NIRS). Neurosci Lett 482:90–94. http://dx.doi.org/10.1016/j.neulet.2010.06.086.
Ikebuchi M, Hasegawa T, Bischof H-J (2009) Amygdala and socio-sexual behavior in male zebra finches. Brain Behav Evol 74:250–257. http://dx.doi.org/10.1159/000264660.
Ikebuchi M, Nanbu S, Okanoya K, Suzuki R, Bischof HJ (2012) Very early development of nucleus taeniae of the amygdala. Brain Behav Evol 81:12–26.
Jarvis CD (1974) Visual discrimination and spatial localization deficits after lesions of the tectofugal pathway in pigeons. Brain Behav Evol 9:195–228.
Jarvis ED, Güntürkün O, Bruce L, Csillag A, Karten H, Kuenzel W, Medina L, Paxinos G, Perkel DJ, Shimizu T, Streidter D, Wild JM, Ball GF, Dugas-Ford J, Durand SE, Hough GE, Husband S, Kubikova L, Lee DW, Mello CV, Powers A, Siang C, Smulders TV, Wada K, White SA, Yamamoto K, Yu J, Reiner A, Butler AB (2005) Avian brains and a new understanding of vertebrate brain evolution. Nat Rev Neurosci 6:151–159. http://dx.doi.org/10.1038/nrn1606.
Johnson MH (2005) Subcortical face processing. Nat Rev Neurosci 6:766–774. http://dx.doi.org/10.1038/nrn1766.
Karten HJ, Hodos W (1967). A stereotaxic atlas of the brain of the pigeon:(Columba Livia), Vol. 696. Baltimore: Johns Hopkins Press.
Karten HJ, Hodos W, Nauta WJH, Revzin AM (1973) Neural connections of the ''visual wulst" of the avian telencephalon. Experimental studies in the pigeon (Columba livia) and owl

(Speotyto cunicularia). J Comp Neurol 150:253–277. http://dx.doi.org/10.1002/cne.901500303.
Kelly AM, Goodson JL (2014) Hypothalamic oxytocin and vasopressin neurons exert sex-specific effects on pair bonding, gregariousness, and aggression in finches. Proc Natl Acad Sci U S A 111:6069–6074. http://dx.doi.org/10.1073/pnas.1322554111.
Klatt JD, Goodson JL (2013) Oxytocin-like receptors mediate pair bonding in a socially monogamous songbird. Proc R Soc Lond B Biol Sci 280:20122396. http://dx.doi.org/10.1098/rspb.2012.2396.
Kleiner M, Brainard D, Pelli D (2007), What's new in Psychtoolbox-3? A free cross-platform toolkit for Psychophysics with Matlab & GNU/Octave.
Kollack-Walker S, Newman SW (1995) Mating and agonistic behavior produce different patterns of Fos immunolabeling in the male Syrian hamster brain. Neuroscience 66:721–736. http://dx.doi.org/10.1016/0306-4522(94)00563-K.
Kollack-Walker S, Newman SW (1997), Mating-induced expression of c-fos in the male Syrian hamster brain: Role of experience, pheromones, and ejaculations.
Kuenzel WJ, Masson M (1988) A stereotaxic atlas of the brain of the chick (Gallus domesticus). London: Johns Hopkins University Press.
Lanahan A, Worley P (1998) Immediate-early genes and synaptic function. Neurobiol Learn Mem 70:37–43. http://dx.doi.org/10.1006/nlme.1998.3836.
Leng G, Meddle SL, Douglas AJ (2008) Oxytocin and the maternal brain. Curr Opin Pharmacol 8:731–734. http://dx.doi.org/10.1016/j.coph.2008.07.001.
Lim MM, Young LJ (2006) Neuropeptidergic regulation of affiliative behavior and social bonding in animals. Horm Behav 50:506–517. http://dx.doi.org/10.1016/j.yhbeh.2006.06.028.
Liu Y, Curtis JT, Wang Z (2001) Vasopressin in the lateral septum regulates pair bond formation in male prairie voles (Microtus ochrogaster). Behav Neurosci 115:910–919. http://dx.doi.org/10.1037/0735-7044.115.4.910.
Maekawa F, Nakamori T, Uchimura M, Fujiwara K, Yada T, Tsukahara S, Kanamatsu T, Tanaka K, Ohki-Hamazaki H (2007) Activation of cholecystokinin neurons in the dorsal pallium of the telencephalon is indispensable for the acquisition of chick imprinting behavior. J Neurochem 102:1645–1657. http://dx.doi.org/10.1111/j.1471-4159.2007.04733.x.
Manns M, Freund N, Patzke N, Güntürkün O (2007) Organization of telencephalotectal projections in pigeons: Impact for lateralized top-down control. Neuroscience 144:645–653. http://dx.doi.org/10.1016/j.neuroscience.2006.09.043.
Martin JT, Delanerolle N, Phillips RE (1979) Avian archistriatal control of fear-motivated behavior and adrenocortical function. Behav Processes 4:283–293. http://dx.doi.org/10.1016/0376-6357(79)90014-7.
Martínez-García F, Novejarque A, Lanuza E (2008) Two interconnected functional systems in the amygdala of amniote vertebrates. Brain Res Bull 75:206–213. http://dx.doi.org/10.1016/j.brainresbull.2007.10.019.
Mascalzoni E, Regolin L, Vallortigara G (2010) Innate sensitivity for self-propelled causal agency in newly hatched chicks. Proc Natl Acad Sci U S A 107:4483–4485. http://dx.doi.org/10.1073/pnas.0908792107.
Mayer U, Bischof H-J (2012) Brain activation pattern depends on the strategy chosen by zebra finches to solve an orientation task. J Exp Biol 215:426–434. http://dx.doi.org/10.1242/jeb.063941.
Mayer U, Pecchia T, Bingman VP, Flore M, Vallortigara G (2016a) Hippocampus and medial striatum dissociation during goal navigation by geometry or features in the domestic chick: An immediate early gene study. Hippocampus 26:27–40. http://dx.doi.org/10.1002/hipo.22486.
Mayer U, Rosa-Salva O, Lorenzi E, Vallortigara G (2016b) Social predisposition dependent neuronal activity in the intermediate medial mesopallium of domestic chicks (Gallus gallus domesticus). Behav Brain Res 310:93–102. http://dx.doi.org/10.1016/j.bbr.2016.05.019.
Mayer U, Rosa-Salva O, Morbioli F, Vallortigara G (2017b) The motion of a living conspecific activates septal and preoptic areas in naive domestic chicks (Gallus gallus). Eur J Neurosci 45:423–432. http://dx.doi.org/10.1111/ejn.13484.
Mayer U, Rosa-Salva O, Vallortigara G (2017a) First exposure to an alive conspecific activates septal and amygdaloid nuclei in visually-naïve domestic chicks (Gallus gallus). Behav Brain Res 317:71–81. http://dx.doi.org/10.1016/j.bbr.2016.09.031.
McCabe BJ (2013) Imprinting. Wiley Interdiscip Rev Cogn Sci 4:375–390. http://dx.doi.org/10.1002/wcs.1231.
McCabe BJ, Horn G (1994) Learning-related changes in Fos-like immunoreactivity in the chick forebrain after imprinting. Proc Natl Acad Sci U S A 91:11417–11421.
McKenzie R, Andrew RJ (1996) Brief retention deficits associated with cyclically recurring left hemisphere events. Physiol Behav 60:1323–1329. http://dx.doi.org/10.1016/S0031-9384(96)00227-2.
McKenzie R, Andrew RJ, Jones RB (1998) Lateralization in chicks and hens: new evidence for control of response by the right eye system. Neuropsychologia 36:51–58. http://dx.doi.org/10.1016/S0028-3932(97)00108-5.
Medina L, Reiner A (2000) Do birds possess homologues of mammalian primary visual, somatosensory and motor cortices? Trends Neurosci 23:1–12. http://dx.doi.org/10.1016/S0166-2236(99)01486-1.
Miura M, Matsushima T (2016) Biological motion facilitates filial imprinting. Anim Behav 116:171–180. http://dx.doi.org/10.1016/j.anbehav.2016.03.025.
Miura M, Matsushima T (2012) Preference for biological motion in domestic chicks: sex-dependent effect of early visual experience. Anim Cogn 15:871–879. http://dx.doi.org/10.1007/s10071-012-0514-x.
Montagnese CM, Székely AD, Ádám Á, Csillag A (2004) Efferent connections of septal nuclei of the domestic chick (Gallus domesticus): An anterograde pathway tracing study with a bearing on functional circuits. J Comp Neurol 469:437–456. http://dx.doi.org/10.1002/cne.11018.
Montagnese CM, Zachar G, Bálint E, Csillag A (2008) Afferent connections of septal nuclei of the domestic chick (Gallus domesticus): A retrograde pathway tracing study. J Comp Neurol 511:109–150. http://dx.doi.org/10.1002/cne.21837.
Newman SW (1999) The medial extended amygdala in male reproductive behavior a node in the mammalian social behavior network. Ann N Y Acad Sci 877:242–257. http://dx.doi.org/10.1111/j.1749-6632.1999.tb09271.x.
Nishizawa K, Izawa E-I, Watanabe S (2011) Neural-activity mapping of memory-based dominance in the crow: neural networks integrating individual discrimination and social behaviour control. Neuroscience 197:307–319. http://dx.doi.org/10.1016/j.neuroscience.2011.09.001.
Northcutt RG (1981) Evolution of the telencephalon in nonmammals. Annu Rev Neurosci 4:301–350. http://dx.doi.org/10.1146/annurev.ne.04.030181.001505.
O'Connell LA, Hofmann HA (2011) The vertebrate mesolimbic reward system and social behavior network: a comparative synthesis. J Comp Neurol 519:3599–3639. http://dx.doi.org/10.1002/cne.22735.
Panzica GC, Bakthazart J, Pessatti M, Viglietti-Panzica C (2002) The parvocellular vasotocin system of Japanese quail: a developmental and adult model for the study of influences of gonadal hormones on sexually differentiated and behaviorally relevant neural circuits. Environ Health Perspect 110:423–428.
Petrulis A (2009) Neural mechanisms of individual and sexual recognition in Syrian hamsters (Mesocricetus auratus). Behav Brain Res 200:260–267. http://dx.doi.org/10.1016/j.bbr.2008.10.027.
Phillips RE (1968) Approach-withdrawal behavior of peach-faced lovebirds, agapornis roseicolis, and its modification by brain lesions. Behaviour 31:163–184. http://dx.doi.org/10.1163/156853968X00045.

Phillips RE, Youngren OM (1971) Brain stimulation and species-typical behaviour: Activities evoked by electrical stimulation of the brains of chickens (Gallus gallus). Anim Behav 19:757–779. http://dx.doi.org/10.1016/S0003-3472(71)80180-X.

Phillips RE, Youngren OM (1986) Unilateral kainic acid lesions reveal dominance of right archistriatum in avian fear behavior. Brain Res 377:216–220. http://dx.doi.org/10.1016/0006-8993(86)90861-9.

Puelles L, Kuwana E, Puelles E, Bulfone A, Shimamura K, Keleher J, Smiga S, Rubenstein JLR (2000) Pallial and subpallial derivatives in the embryonic chick and mouse telencephalon, traced by the expression of the genes Dlx-2, Emx-1, Nkx-2.1, Pax-6, and Tbr-1. J Comp Neurol 424:409–438.

Reiner A, Karten HJ (1983) The laminar source of efferent projections from the avian Wulst. Brain Res 275:349–354. http://dx.doi.org/10.1016/0006-8993(83)90996-4.

Reiner A, Perkel DJ, Bruce LL, Butler AB, Csillag A, Kuenzel W, Medina L, Paxinos G, Shimizu T, Streidter G, Wild M, Ball GF, Durand S, Güntürkün O, Lee DW, Mello CV, Powers A, White SA, Hough G, Kubikova L, Smulders TV, Wada K, Dugas-Ford J, Husband S, Yamamoto K, Yu J, Siang C, Jarvis ED (2004) Revised nomenclature for avian telencephalon and some related brainstem nuclei. J Comp Neurol 473:377–414. http://dx.doi.org/10.1002/cne.20118.

Riters LV, Absil P, Balthazart J (1998) Effects of brain testosterone implants on appetitive and consummatory components of male sexual behavior in Japanese quail. Brain Res Bull 47:69–79.

Rogers LJ, Anson JM (1979) Lateralisation of function in the chicken fore-brain. Pharmacol Biochem Behav 10:679–686. http://dx.doi.org/10.1016/0091-3057(79)90320-4.

Rogers LJ, Vallortigara G, Andrew RJ (2013) Divided Brains. The biology and Behaviour of Brain Asymmetries. Cambridge, UK: Cambridge University Press.

Rogers LJ, Zappia JV, Bullock SP (1985) Testosterone and eye-brain asymmetry for copulation in chickens. Experientia 41:1447–1449. http://dx.doi.org/10.1007/BF01950028.

Rosa-Salva O, Mayer U, Vallortigara G (2015) Roots of a social brain: Developmental models of emerging animacy-detection mechanisms. Neurosci Biobehav Rev 50:150–168. http://dx.doi.org/10.1016/j.neubiorev.2014.12.015.

Rosa-Salva O, Regolin L, Mascalzoni E, Vallortigara G (2012b) Cerebral and behavioural asymmetries in animal social recognition. Comp Cogn Behav Rev 7:110–138.

Rosa-Salva O, Regolin L, Vallortigara G (2007) Chicks discriminate human gaze with their right hemisphere. Behav Brain Res 177:15–21. http://dx.doi.org/10.1016/j.bbr.2006.11.020.

Rosa-Salva O, Daisley JN, Regolin L, Vallortigara G (2009) Lateralization of social learning in the domestic chick, Gallus gallus domesticus: learning to avoid. Anim Behav 78:847–856. http://dx.doi.org/10.1016/j.anbehav.2009.06.021.

Rosa-Salva O, Farroni T, Regolin L, Vallortigara G, Johnson MH (2011) The evolution of social orienting: evidence from chicks (gallus gallus) and human newborns. PLoS One 6:e18802. http://dx.doi.org/10.1371/journal.pone.0018802.

Rosa-Salva O, Grassi M, Lorenzi E, Regolin L, Vallortigara G (2016) Spontaneous preference for visual cues of animacy in naïve domestic chicks: The case of speed changes. Cognition 157:49–60. http://dx.doi.org/10.1016/j.cognition.2016.08.014.

Rosa-Salva O, Regolin L, Vallortigara G (2010) Faces are special for newly hatched chicks: evidence for inborn domain-specific mechanisms underlying spontaneous preferences for face-like stimuli. Dev Sci 13:565–577. http://dx.doi.org/10.1111/j.1467-7687.2009.00914.x.

Rosa-Salva O, Regolin L, Vallortigara G (2012a) Inversion of contrast polarity abolishes spontaneous preferences for face-like stimuli in newborn chicks. Behav Brain Res 228:133–143. http://dx.doi.org/10.1016/j.bbr.2011.11.025.

Rugani R, Rosa-Salva O, Regolin L, Vallortigara G (2015) Brain asymmetry modulates perception of biological motion in newborn chicks (Gallus gallus). Behav Brain Res 290:1–7.

Ruscio MG, Adkins-Regan E (2004) Immediate early gene expression associated with induction of brooding behavior in Japanese quail. Horm Behav 46:19–29. http://dx.doi.org/10.1016/j.yhbeh.2004.02.002.

Sadananda M, Bischof H-J (2004) C-fos is induced in the hippocampus during consolidation of sexual imprinting in the zebra finch (Taeniopygia guttata). Hippocampus 14:19–27. http://dx.doi.org/10.1002/hipo.10149.

Sheehan T, Paul M, Amaral E, Numan MJ, Numan M (2001) Evidence that the medial amygdala projects to the anterior/ventromedial hypothalamic nuclei to inhibit maternal behavior in rats. Neuroscience 106:341–356. http://dx.doi.org/10.1016/S0306-4522(01)00286-X.

Sheng M, Greenberg ME (1990) The regulation and function of c-fos and other immediate early genes in the nervous system. Neuron 4:477–485.

Simion F, Regolin L, Bulf H (2008) A predisposition for biological motion in the newborn baby. Proc Natl Acad Sci U S A 105:809–813. http://dx.doi.org/10.1073/pnas.0707021105.

Slawski BA, Buntin JD (1995) Preoptic area lesions disrupt prolactin-induced parental feeding behavior in ring doves. Horm Behav 29:248–266. http://dx.doi.org/10.1006/hbeh.1995.1018.

Solomonia RO, McCabe BJ, Horn G (1998) Neural cell adhesion molecules, learning, and memory in the domestic chick. Behav Neurosci 112:646–655. http://dx.doi.org/10.1037/0735-7044.112.3.646.

Solomonia RO, McCabe BJ, Jackson AP, Horn G (1997) Clathrin proteins and recognition memory. Neuroscience 80:59–67. http://dx.doi.org/10.1016/S0306-4522(97)00123-1.

Sugita Y (2008) Face perception in monkeys reared with no exposure to faces. Proc Natl Acad Sci U S A 105:394–398. http://dx.doi.org/10.1073/pnas.0706079105.

Taziaux M, Cornil CA, Dejace C, Arckens L, Ball GF, Balthazart J (2006) Neuroanatomical specificity in the expression of the immediate early gene c-fos following expression of appetitive and consummatory male sexual behaviour in Japanese quail. Eur J Neurosci 23:1869–1887. http://dx.doi.org/10.1111/j.1460-9568.2006.04719.x.

Taziaux M, Keller M, Ball GF, Balthazart J (2008) Site-specific effects of anosmia and cloacal gland anesthesia on Fos expression induced in male quail brain by sexual behavior. Behav Brain Res 194:52–65. http://dx.doi.org/10.1016/j.bbr.2008.06.022.

Thompson R, Goodson JL, Ruscio MG, Adkins-Regan E (1998) Role of the archistriatal nucleus taeniae in the sexual behavior of male japanese quail (Coturnix japonica): a comparison of function with the medial nucleus of the amygdala in mammals. Brain Behav Evol 51:215–229. http://dx.doi.org/10.1159/000006539.

Tremoulet PD, Feldman J (2000) Perception of animacy from the motion of a single object. Perception 29:943–951.

Vallortigara G (1992) Right hemisphere advantage for social recognition in the chick. Neuropsychologia 30:761–768. http://dx.doi.org/10.1016/0028-3932(92)90080-6.

Vallortigara G, Andrew RJ (1991) Lateralization of response by chicks to change in a model partner. Anim Behav 41:187–194. http://dx.doi.org/10.1016/S0003-3472(05)80470-1.

Vallortigara G, Andrew RJ (1994) Differential involvement of right and left hemisphere in individual recognition in the domestic chick. Behav Proc 33:41–58.

Vallortigara G, Cozzutti C, Tommasi L, Rogers LJ (2001) How birds use their eyes: Opposite left-right specialization for the lateral and frontal visual hemifield in the domestic chick. Curr Biol 11:29–33. http://dx.doi.org/10.1016/S0960-9822(00)00027-0.

Vallortigara G, Regolin L (2006) Gravity bias in the interpretation of biological motion by inexperienced chicks. Curr Biol 16: R279–R280. http://dx.doi.org/10.1016/j.cub.2006.03.052.

Vallortigara G, Versace E (2017), Laterality at the Neural, Cognitive, and Behavioral Levels. In "APA Handbook of Comparative Psychology: Vol. 1. Basic Concepts, Methods, Neural Substrate, and Behavior", J. Call (Editor-in-Chief), pp. 557–577, American Psychological Association, Washington DC.

Vallortigara G, Regolin L, Marconato F (2005) Visually inexperienced chicks exhibit spontaneous preference for biological motion

patterns. PLoS Biol 3:e208. http://dx.doi.org/10.1371/journal.pbio.0030208.
Verhaal J, Luksch H (2015) Processing of motion stimuli by cells in the optic tectum of chickens. Neuroreport 26:578–582. http://dx.doi.org/10.1097/WNR.0000000000000391.
Versace E, Fracasso I, Baldan G, Dalle Zotte A, Vallortigara G (2017) Newborn chicks show inherited variability in early social predispositions for hen-like stimuli. Sci Rep 7:40296. http://dx.doi.org/10.1038/srep40296.
Versace E, Schill J, Nencini AM, Vallortigara G (2016) Naïve chicks prefer hollow objects. PLoS One 11(11):e0166425. http://dx.doi.org/10.1371/journal.pone.0166425.
Versace E, Vallortigara G (2015) Origins of knowledge: Insights from precocial species. Front Behav Neurosci 9:338. http://dx.doi.org/10.3389/fndeh.2015.00338.
Walls LG (1942) The vertebrate eye and its adaptive radiation. Oxford, England: Cranbrook Institute of Science.
Wild JM, Williams MN (2000) Rostral Wulst in passerine birds. I. Origin, course, and terminations of an avian pyramidal tract. J Comp Neurol 416:429–450.
Xin Q, Ogura Y, Uno L, Matsushima T (2016) Selective contribution of the telencephalic arcopallium to the social facilitation of foraging efforts in the domestic chick. Eur J Neurosci. http://dx.doi.org/10.1111/ejn.13475.
Yamamoto K, Reiner A (2005) Distribution of the limbic system-associated membrane protein (LAMP) in pigeon forebrain and midbrain. J Comp Neurol 486:221–242. http://dx.doi.org/10.1002/cne.20562.
Yamamoto K, Sun Z, Wang HB, Reiner A (2005) Subpallial amygdala and nucleus taeniae in birds resemble extended amygdala and medial amygdala in mammals in their expression of markers of regional identity. Brain Res Bull 66:341–347. http://dx.doi.org/10.1016/j.brainresbull.2005.02.016.
Zachar G, Schrott A, Kabai P (2008) Context-dependent prey avoidance in chicks persists following complete telencephalectomy. Brain Res Bull 76:289–292. http://dx.doi.org/10.1016/j.brainresbull.2008.02.017.

(Received 22 December 2016, Accepted 17 April 2017)
(Available online 25 April 2017)