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Research report

First exposure to an alive conspecific activates septal and amygdaloid nuclei in visually-naïve domestic chicks *(Gallus gallus)*

Dr. rer. nat. Uwe Mayer*, Orsola Rosa-Salva, Giorgio Vallortigara

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

HIGHLIGHTS

- Septal and amygdaloid nuclei are involved in social behavior of adult animals.
- Here we investigated their involvement in early social responses of visually naive chicks.
- Higher activity in septum and amygdaloid nuclei of chicks after the first brief exposure to an alive conspecific.

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ABSTRACT

The septal nuclei are an evolutionarily well-conserved part of the limbic system, present in all vertebrate groups. Functionally, septal nuclei are involved in many important aspects of social behavior and lateral septum is considered a node of the social decision making network, together with amygdaloid nuclei. Given the importance of septal nuclei for social behaviors, it is somewhat surprising that it has never been investigated whether they are involved in early social responses of naïve animals. In the present study we wanted to know if simple exposure of visually naïve newly hatched chicks to a visual object (an alive, behaving conspecific), that also contains all features to which chicks are known to express early social predispositions, will selectively activate septal areas. We measured brain activity by visualizing the immediate early gene product c-Fos with a standard immunohistochemical procedure. Notably, after a brief visual exposure to an alive behaving conspecific septum showed higher activation in experimental subjects, compared to baseline animals that were exposed to the same environment in the absence of the conspecific. This is, to the best of our knowledge, the first demonstration of septal involvement in early social responses. We also found similar effects in the nucleus taeniae and arcopallium (amygdala homologues), but not in the medial striatum. This result indicates that at least some nuclei of the social decision making network may participate in early responses to social stimuli. Future studies could capitalize on these results, by identifying the specific visual cues eliciting this effect.

1. Introduction

The septal nuclei are an evolutionarily well-conserved part of the limbic system, present in all vertebrate groups [1]. In mammals, septum is located medial to the lateral ventricles and is anatomically and functionally connected to the hippocampus [2]. It is also interconnected with the hypothalamic nuclei that are relevant for social behaviors, such as the preoptic area (POA), the anterior hypothalamus (AH), the ventromedial hypothalamus (VMH) [3–5] and it also projects to the midbrain [6]. Septum receives inputs from further social brain regions, such as the bed nucleus of stria terminalis (BNST), the medial amygdala [7–9] and dopaminergic projections from the ventral tegmental area (VTA) [10]. Many studies in mammals have implicated the lateral septum in a variety of social behaviors, such as social memory, individual recognition, dominance hierarchies, territoriality, aggression, sexual behavior, pair-bond, parental and anxiety-related behaviors, which are mainly mediate through neuropeptide signaling based on vasopressin and oxytocin receptors [11–29].

Similar to the mammalian septum, its avian homolog is located medial to the lateral ventricles and it also shares the connectivity profile of the mammalian septum, with massive inputs from the hippocampus and projections to the hypothalamus and midbrain [30–34]. It contains dense dopaminergic fibers [35] and shows subdivisional organization that resembles that of the mammalian septum [36]. Similarities between mouse and domestic chick's dorsal (pallial) and ventral (subpallial) portions of the septum

* Corresponding author at: Center for Mind/Brain Sciences, University of Trento, Piazza Manifattura 1, I-38068, Rovereto (TN) Italy.
E-mail address: uwe.mayer@unitn.it (U. Mayer).

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have been confirmed by comparative examination of developmental gene expression [37,38]. Research on the functions of the avian septum is generally sparse and not all functions known in mammals have been investigated in birds. However, besides a few studies that targeted septal involvement in spatial memory [39–41], most investigations have focused on regulation of social behaviors and have uncovered similarities to mammalian species [42,43]. In adult birds septal nuclei participate in territorial behavior, aggression, dominance hierarchies, individual discrimination, social communication, pair-bonding, gregariousness, appetitive and consummatory sexual behaviors [42,44–58]. Similar to mammals, some of these behaviors are mediated by arginine vasotocin (AVT, homologous to arginine vasopressin in mammals) [46]. The AVT-ir fibers are dense in the lateral portion of the avian septum [36], showing that the avian lateral septum is also functionally similar to the lateral septum in mammals. In fact, some studies also found localized involvement of the avian lateral septum in social functions (aggression and sexual behavior) [56,57].

As in mammals, the lateral septum in birds is considered one of the nodes of the social behavior network [42,59], which exhibits extensive similarities between the two taxa in its connections, histochemistry, and locations of sex steroid receptors [30,33,34,36,53,60–66]. These nodes by definition are in control of multiple forms of social behavior, they contain sex steroids receptors and are reciprocally interconnected [59]. The participation of this network in regulation of social behaviors in birds and mammals have been studied on the basis of immediate early gene induction, revealing similar patterns of activity [18–20,36,46,67–81]. The expressions of these genes are reliably induced by behaviorally relevant neuronal activity and their products have often been used to map brain activities in different species [39,82–89]. The lateral septum is also connected to the mesolimbic reward system, which makes it to an important key element in a larger social decision making network [90].

Other important elements of the social decision making network are the nuclei of the amygdala, which have also been theorized to support early responses to social stimuli, e.g. attention to faces in human newborns [91]. In mammals, amygdala is composed by pallial parts such as the lateral, basolateral, basomedial and cortical nuclei and subpallial parts such as the central and medial nuclei [92]. While the medial amygdala, similar to lateral septum, interconnects the social behavior network and the mesolimbic rewards network, the basolateral amygdala represents a part of the latter [90]. The medial amygdala plays a particularly important role in mediating sexual responses and regulates appetitive responses (e.g., see [93–98]). In birds, after a recent nomenclature change and reinterpretation of the telencephalon [99,100], two regions were classified as subpallial amygdaloid nuclei, the nucleus taeniae of the amygdala (TnA) and the newly identified subpallial amygdala (SpA). Neuroanatomical studies suggested that the avian nucleus taeniae of the amygdala (TnA) might be homologous to mammalian medial amygdala [101]. Like its mammalian counterpart, the TnA receives direct inputs from olfactory bulb [102,103] and sends hippocampal and hypothalamic output [64,104,105]. This area shows an enrichment in androgen and estrogen receptors [106–109] and is in control of different social functions, such as sexual behaviors and social interactions [64,67,80,110]. In an altricial species the zebra finch, TnA can already be delineated at post hatching day one [111], which supports the idea that the early development of TnA is necessary for social control already at the time of hatching.

The homologies of the pallial structures of the amygdala in the bird's brain are more complicated. Some authors propose that the whole dorsal ventricular ridge (DVR) of birds is exclusively homologous to the mammalian basolateral amygdala, endopiriform nucleus, and/or claustrum [38,112–117]. This view is challenged by the "neocortical hypothesis", which considers the mesopallium (M), nidopallium (N) and arcopallium (A) to be of cortical origin and is supported by hodological, morphological, histochemical and topological observations [118,119]. According to the classical view by Zeier and Karten [120], the arcopallium (old name 'archistriatum', [100]) is composed of a limbic, amygdaloid part that projects to the hypothalamus and includes nucleus taeniae of the amygdala (TnA) and the posterior amygdala (PoA). The other part of arcopallium is a somatomotoric part and is composed of anterior arcopallium (AA), dorsal arcopallium (AD) and the dorsal part of the ventral arcopallium (AV). The ventropallial olfactory-related origin of the arcopallium is confirmed by more recent studies on its connections [121]. It is worth mentioning that several classical lesioning and electrical stimulation studies have implicated the caudal and medial arcopallium (archistriatum) in fear related behaviors in different birds [122–126], which show that at least some parts of arcopallium have similar functions to the mammalian pallial amygdala.

Given the importance of septal and amygdaloid nuclei for social functions, it is surprising that so far no studies investigated their involvement in early social behaviors of newborn animals. Early social behaviors are believed to play a crucial role in the ontogenesis of social cognition, in both human and non-human primates [91,127] and in avian species [128]. Newborn vertebrates of these distant species show early predispositions to attend to socially relevant stimuli, which bias their early experiences in favor of certain classes of stimuli. This could have a crucial role in shaping the normal development of social function and the related neural circuitry [129]. Domestic chicks are an ideal model to investigate questions related to early social responses [130]. Being the precocial offspring of a social species, chicks allow to test social behavior while strictly controlling pre- and post-hatching experiences. Soon after hatching, before any learning about social stimuli occurs, nidifugous chicks of gallinaceous species are already predisposed to respond to social stimuli [128]. These early predispositions will ensure subsequent imprinting towards appropriate social objects. Filial imprinting involves individual recognition of the imprinting object and social bonding to it [131]. In a natural environment the imprinting object could be either the mother hen or a sibling (another chick of the same hatch). These features allow to use chicks as a model to study the role of experience in septal and amygdaloid responses to social objects. Are these areas involved in social functions immediately after birth/hatching or is postnatal visual learning and experience required to recruit them? In the present study we thus investigated septal activity of visually naïve chicks after the first brief visual exposure to an alive, behaving conspecific and compared it to a baseline group of chicks that were exposed to the same visual and acoustical environment, but without visual exposure to the alive conspecific. We measured neuronal activity in the brain areas of interest by labelling the immediate early gene product c-Fos with a standard immunohistochemical procedure. We hypothesized that seeing a conspecific will selectively upregulate septal activity in the experimental group. We also measured neuronal activity in nucleus taeniae (TnA) and arcopallium (A). As a control region we measured activity in the medial striatum (MStr), lobus parolfactorius, LPO according to the old nomenclature, [99].

2. Material and methods

2.1. Subjects

Thirty laboratory-hatched, domestic chicks (*Gallus gallus domesticus*), of the "Hybro strain" (a local variety derived from the white leghorn breed), were used. Fertilized eggs were obtained from a local commercial hatchery (Agricola Berica, Montegalda (VI), Italy) and were hatched in groups inside dark incubators