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Abstract	Crows, a highly social bird, live in a complex 'fission-fusion' society where individuals need to recognize identity of group members with forming social relationships such as dominance. Such social nature could predict the existence of the integrative brain mechanisms for individual recognition and dominance relationships. Despite a number of evidence for the sophisticated cognitive abilities of this species, little has been unknown on the neural basis for social cognition. In this study, to clarify how to integrate individual recognition, dominance, and behavioral expression, we investigated pallial-limbic system including association pallium, striatum, and hypothalamus by analyzing expression of immediate early gene ZENK, an indirect neuronal activity marker. Firstly, the formation of stable dominance relationships based on the individual recognition was confirmed between male jungle crows in a dyadic encounter paradigm. Then the neuronal activities during an exposure session where each subject crow was exposed to either of a familiar dominant, subordinate, or an unfamiliar 'stuff' crow as a stimulus. To evaluate the multiple contributions of each brain area to cognitive/behavioral aspects, ZENK expression was analyzed by means of a generalized regression model (GdML) base on multi-ple factors such as familiarity, dominance, and non-specific actions of the stimulus crow. Neuronal correlation to familiarity was found mainly in association pallium, whereas that to aggression was found in sub-pallial areas. Hippocampal complex and septal nuclei, furthermore, showed multiple contribution to the factors. Given those results together with the past anatomical studies, we could propose a hypothetical neural system, 'association pallium – parahippocampal – septal subdivisions,' for dominance recognition.
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6 Neural System for Integrating Individual Recognition and Dominance Relationship in Crows

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Summary

Crows, a highly social bird, live in a complex 'fission-fusion' society where individuals need to recognize identity of group members with forming social relationships such as dominance. Such social nature could predict the existence of the integrative brain mechanisms for individual recognition and dominance relationships. Despite a number of evidence for the sophisticated cognitive abilities of this species, little has been unknown on the neural basis for social cognition. In this study, to clarify how to integrate individual recognition, dominance, and behavioral expression, we investigated pallial-limbic system including association pallium, striatum, and hypothalamus by analyzing expression of immediate early gene ZENK, an indirect neuronal activity marker. Firstly, the formation of stable dominance relationships based on the individual recognition was confirmed between male jungle crows in a dyadic encounter paradigm. Then the neuronal activities during an exposure session where each subject crow was exposed to either of a familiar dominant, subordinate, or an unfamiliar 'stuff' crow as a stimulus. To evaluate the multiple contributions of each brain area to cognitive/behavioral aspects, ZENK expression was analyzed by means of a generalized regression model (GdML) base on multi-

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I. Introduction

The jungle crow (*Corvus macrorhynchos*), a highly social bird, live in a complex society which requires individuals to recognize group members and their social relationships (Emery and Clayton, 2004). To survive in such complex societies, individuals should have the cognitive abilities to associate 'individual identity' and 'social relationships' among group members. Indeed, we found that crows established the stable dominance relationships at the first encounters and, subsequently, maintained the dominant or subordinate relationships discriminatively to the opponents (Izawa and Watanabe, 2008). Such social nature of crows could provide the advantages to understand the neural system as a model for social adaptation.

Despite a number of behavioural evidence for the sophisticated socio-cognitive abilities of crows and the related species (Emery and Clayton, 2004), little has been known about the neural substrates except for several studies using volumetric analyses (Izawa and Watanabe, 2007; Cnotka et al., 2008). Regarding to the social behavior, previous studies on small birds reported the critical role of limbic subpallial structures such as septum and hypothalamus (Mello et al., 1992; Thompson et al., 1998; Goodson et al., 1999, 2004, 2005). These previous studies, however, paid attentions only to the output of social cognition such as aggression and avoidance behaviour but not to the integrative processes such as individual recognition.

In this study, we investigated the brain areas involved in the integration between dominance-specific behavioral output and individual recognition in the crow. To determine the relevant brain area to such social recognition process, we evaluated the expression of ZENK protein, a product of immediate early gene, as an indirect neuronal activity marker between the different social situations where subjects encountered familiar/unfamiliar individuals with dominant/subordinate relationships.

II. Materials & Methods

1. Behavioral Experiment

Firstly, we confirmed the formation of dominance relationships between male jungle crows in a pairwise encounter paradigm which was employed in our previous study (Izawa and Watanabe, 2008). In this behavioral paradigm, pairs of male crows were given the opportunities to encounter three times successively with 1-day intervals in an open arena (1.7 x 1.2 m^2). We expected the reduction of aggressive level specifically against the same opponents in the 2nd and/or 3rd encounters if crows established dominance relationships on the basis of the memory of win/loss outcomes associated with the specific individuals in the 1st encounters.

2. Immuno-histochemical Assessment

After confirming the formation of dominance relationships based on individual recognition, subjects were exposed to either of a dominant, a subordinate, or an unfamiliar 'stuff' crow for a 30-min session. One hour after the end of the exposure session, the expression of ZENK gene (homologue to zif-268 gene in mammals), an indirect gene marker of neuronal activities, in brain nuclei were measured by means of typical immuno-histochemical technique (Mello et al., 1992) to assess the relevant brain nuclei to social recognition.

Particular attention was paid to limbic-pallial system including association areas in pallium (i.e., HA, apical part of the hyperpallium; HD, densocelluer part of the hyperpallium; MM, medial mesopallium; CMM, caudo-medial mesopallium; NCL, caudo-lateral nidopallium; NCM, caudo-medial nidopallium), limbic subpallium (MSt, medial striatum; Hp, hippocampus; APH, area parahippocampus; BST, bed nucleus striae terminalis), and hypothalamic nuclei (MS, medial septum; LSc. dl/dm/vl, subdivisions of lateral septum). References of each brain nuclei were according to a brain atlas of the crow (Izawa and Watanabe, 2007) and those of subdivisions, especially septal nuclei, were followed to the previous studies on zebra finches (Thompson et al., 1998; Goodson et al., 1999)

3. Analysis

To determine the involvement of brain areas involved in social recognition, we examined the correlation of neuronal activities in focal brain nuclei to social and/or behavioral factors by using a multivariable regression analysis, generalized regression model (GdLM). The degree of ZENK expression was considered as dependent variable to be explained by several independent factors and variables such as a factor of 'familiarity' of stimulus crows, variables of the number of 'aggression' and 'submission' behavior, and 'nonspecific behavior' of the subjects during exposure sessions. ZENK expression as an index of neuronal activity of each focal nucleus was standardized as a ratio value to that of optic tectum. The numbers of each type of behavior were z-transformed to be normalized across subjects. Selection of the best-fitted final model was executed by subsequently reducing a factor/variable from the initial full model until the smallest value of Akaike Information Criterion (AIC) was attained. For this procedure, we did not consider any levels of interaction between the factor and variables but rather examined the contribution of single factor and variable. A statistical free-software 'R (ver. 2.9.1)' was used for the analysis.

III. Results

1. Behavioral Experiment

Consistently with our previous study (Izawa and Watanabe, 2008), in the behavioral experiment, drastic reduction of the aggressive level was found across the repeated encounters with the same opponents. Figure 1 showed that aggressive interactions occurred only in the 1st encounters and drastically decreased in the 2nd and the 3rd ones. Such low level of aggression after establishing dominance relationships in the 1st encounter was maintained in the test session. Such decrease of aggression across the repeated encounters was not observed when the opponents were different (Figure 2), indicating that the reduction of aggressive level in Figure 1 occurred in the subsequent encounters specifically with the same opponents. These data indicated that crows determined the winner or loser not on an event-to-event basis but on the dominance relationships which were established in the 1st encounters, implying the involvement of individual recognition in maintaining the dominance relationships.

These behavioral results suggest a possibility of neural system to integrate individual recognition and dominance relationships.

2. Neuronal Correlation to Social Recognition

Analysis of neuronal activities during exposure session in focal brain areas suggests the multiple involvements of different brain areas in social recognition. The results of the multi-level involvement of focal nuclei areas in social recognition are

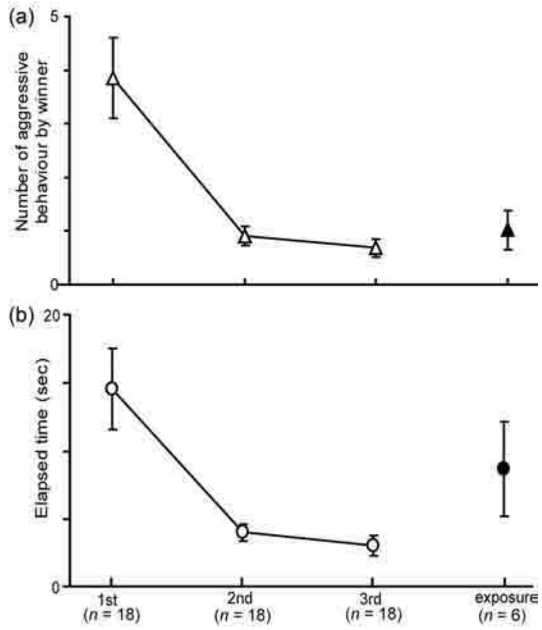

Figure 1. The level of aggression decreased across the successive encounters with the same opponents.

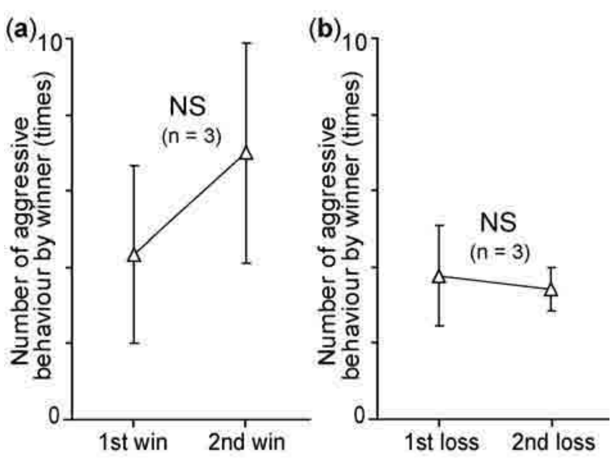

Figure 2. The decease of aggression level was not found between the subsequent encounters with the different opponents.

Table 1. Results of generalized liner model (GdLM)

** > 0.01, * > 0.05, † > 0.1

brain nucleus	Coefficients						Residual deviance	d.f.	AIC
	(Intercept)	familiarity	aggression	submission	total number of action	hearing			
limbic subpallium									
LSc.dl	-0.389	-	1.680 *	1.168	-0.774 †	-1.030 *	1.399	4	20.784
LSc.dm	0.895 *	-1.262 *	0.455	-1.423 *	-0.548 *	-	0.784	4	15.576
LSc.vl	0.498	-0.848	0.078 †	0.367	-0.636 †	-0.553	0.512	3	13.737
MS	-0.391	-	1.720 **	1.175	-0.747 *	-1.061 *	1.063	4	18.312
TnA	0.186	-0.559	0.438	-	-0.520	-	2.167	5	22.726
BST	1.094	-1.310	-0.506	-1.973 †	-	-	4.225	5	28.735
posterior Hp	-0.280	0.840 †	0.981 **	-	-0.804 *	-	1.408	5	18.846
anterior Hp	1.097	-1.061	0.167	0.186	-	0.166	4.317	4	30.929
anterior APH	0.406	-	-	-1.219 *	-	0.639 *	2.849	6	23.188
pallium									
medial NCM	-0.352	-	-	1.055	-	-	5.774	7	27.547
dorsal NCM	-0.429	-	0.806	1.288	-0.764	-0.932	2.875	4	27.270
NCL	0.440	-1.321 *	-	-	-0.434 †	-	2.153	6	20.667
NCv	0.296	-0.889	1.026 *	-	-0.662 †	-0.694 †	1.554	4	21.734
CMM	1.678 †	-1.846	-1.316	-3.188 †	0.409	1.279 †	1.890	3	25.496
PoA	0.607 †	-0.506	-1.569 **	-1.313 *	1.372 **	0.927 *	0.201	3	5.337
MM	0.427	-	-	-1.280 *	-0.849 *	-	2.413	6	21.692
MN	0.247	-0.740	0.467	-	-0.791	-0.665	2.483	4	25.953
LM	0.000	-	-	-	-0.638 †	-	4.747	7	25.784
LN	0.000	-	-	-	-0.521	-	5.827	7	27.628
HA	-0.439	-	-	1.320 †	-	-	4.518	7	25.339
HD	-0.200	-	-	0.601	-0.621 *	0.268	1.775	5	20.929
subpallium									
AreaX	-0.363	1.088	0.650	-	-0.448	-	4.121	5	28.510
MSt dm	0.000	-	0.971 †	-	-0.098 *	-0.976 *	2.647	5	24.525

summarized in Table 1.

Neuronal responses to familiarity factors were found in association pallium NCL and also limbic sub-pallium nuclei such as posterior Hp and LSc. dm. Correlations to aggressive- and/or submissive-behavior were observed in NCv, MM, and HA in pallium, and also anterior APH, posterior Hp, LSc., MS, BST, and MSt in sub-pallium. Although PoA exhibited both aggression and submission behavior, it might be reflected by the involvement of this nucleus in nonspecific behavior.

IV. Discussion & Conclusion

In the present study, we found neuronal activities of pallial and sub-pallial nuclei which were related to social recognition based on individual recognition and aggressive-/submissive-behavioral output.

Our findings provide a possibility that hippocampal complex and its reciprocally connected LS could play a role as an interface in associating 'individual recognition' and 'dominance relationship.' Neuronal activities in posterior Hp and LSc. dm showed the correlation to both familiarity of stimulus crows and aggression/submission behavior of subject crows. Familiarity factor, a mnemonic aspect relevant to individual recognition, was represented not in subpallium but only in

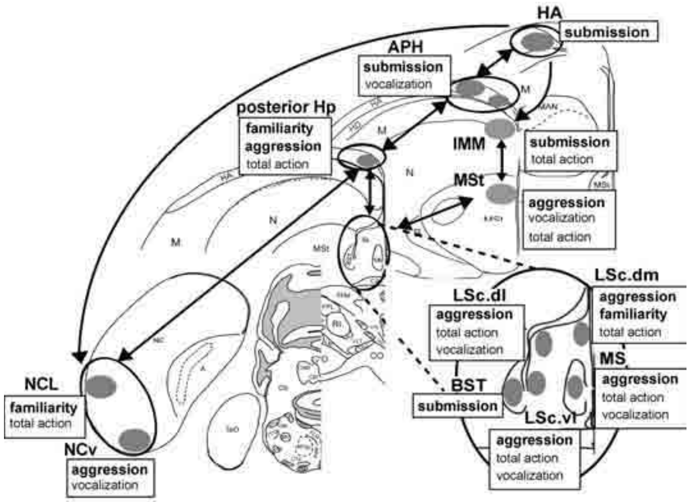

Figure 3. A hypothetical neural system to integrate individual recognition and behavioral output of aggression and submission.

association pallium NCv. On the other hand, subpallial nuclei such as LSc and MS showed the correlation to behavioral output of aggression and submission. These differential neuronal responses to multiple factor/variables with some overlaps might make sense when considering the anatomical connections between those nuclei which were demonstrated in the past anatomical studies in birds (Kröner and Güntürkün, 1999; Atoji and Wild, 2007). Given the present results together with these anatomical studies of avian brain, we can propose a hypothetical system to dominance-relationship formation/maintenance, namely integration between individual recognition and behavioral output of aggression and submission, like as shown in Figure 3. In this system, aggressive- or submissive-behavioral output was controlled in LSc dependently on the individual recognition processed in association pallum NC, via hippocampal formation as an interface between NC and LSc.

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