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研究課題名（和文）脳内甲状腺ホルモンによる鳥類早期学習プライミング機構の解明

研究課題名（英文）Memory priming of filial imprinting by the action of thyroid hormone in domestic chicks

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研究成果の概要（和文）：刷り込みの神経伝達機構と解剖学的基盤を明らかにすることで、ニワトリヒナ脳内甲状腺ホルモンによる学習プライミング機構を解明する業績を達成した。ムスカリン性アセチルコリン受容体が刷り込みに必要であることを示した。胎生期にニコチン性アセチルコリン伝達を遮断するとヒナのバイオロジカルモーションに障害が生じることを示した。中脳のドーパミン性神経核や海馬には、セロトニン受容体サブファミリー遺伝子群が発現していることを示した。脳スライスを用いて、甲状腺ホルモンによる抑制的な電気生理学的調節機構を明らかにした。刷り込み学習をミリ秒単位で解析できる新しい行動装置を開発した。

研究成果の学術的意義や社会的意義
これまで刷り込みは離巣性鳥類の親を覚える特殊な記憶学習であり、その後の個体発生の種々の学習に影響を及ぼす学習とは考えられていなかった。しかし、代表者らの研究の結果、学習に伴って脳内に流入する甲状腺ホルモンによってニワトリヒナの刷り込み学習が可能になると、その後の学習の習得力が飛躍的に向上することがわかった。本研究は、学習臨界期中に遷移する神経回路のキー分子として甲状腺ホルモンに焦点を当て、新たに開発した行動装置を利用して研究を遂行する独自性の高いものであり、視覚優先学習と聴覚優先学習における脳機能を比較しながら脳の機能的進化を考察できる点において、国内外の研究にはない視点と成果が期待できる。

研究成果の概要（英文）：Blockade of muscarinic acetylcholine receptor impaired imprinting. The dorsal arcopallium of chicks displayed the expression of orthologs of mammalian fear-related serotonin receptor subfamily genes. Fetal blockade of nicotinic acetylcholine transmission caused autism-like impairment of biological motion preference. Dopaminergic nuclei in the chick midbrain expressed serotonin receptor subfamily genes. Muscarinic acetylcholine receptors contributed subtype-selectively for imprinting. Thyroid hormone modulated the chick forebrain network for imprinting. Chick hippocampus displayed subdivision- and layer-selective expressions of serotonin receptor genes. The imprintability of newly hatched chicks was assessed by a high-time resolution apparatus based on a running disc.

研究分野：動物生理化学

キーワード：刷り込み　甲状腺ホルモン　早期学習　プライミング　ニワトリ

１．研究開始当初の背景

研究期間全体で、孵化直後のニワトリヒナが示す親子刷り込みの神経伝達機構と解剖学的基盤を明らかにすることで、脳内甲状腺ホルモンによる鳥類早期学習プライミング機構を解明する業績を達成した。１０報の研究業績それぞれについて、「研究背景」と「目的、方法、成果」に分けて記す。

① Imprintability of newly hatched domestic chicks

In filial imprinting, newly hatched chicks repeatedly approach a conspicuous object nearby and memorize it, even though it is an artificial object instead of their mother hen. Imprinting on an artificial object in a laboratory setting has a clear sensitive period from post hatch days 1-3 in the case of domestic chicks. However, the establishment of imprintability are difficult to investigate because of the limitations of the behavioral apparatus.

② Muscarinic acetylcholine receptors in the memory formation of imprinting

Filial imprinting in precocial birds is a useful model for studying memory formation in early learning. The intermediate medial mesopallium (IMM) in the dorsal telencephalon is one of the critical brain regions where the releases of several neurotransmitters increase after the start of imprinting training. Among the increased neurotransmitters, the role of acetylcholine in imprinting has remained unclear. Acetylcholine in the mammalian brain plays an important role in encoding new memories. The muscarinic acetylcholine receptor subtype 1 (M1 receptor) and subtype 3 (M3 receptor) in the hippocampus and cortex of mammalian brain have been shown to be necessary for memory encoding.

③ Subtype-selective contribution of muscarinic acetylcholine receptors for imprinting

Muscarinic acetylcholine receptors (mAChRs) play an important role in many brain functions. Our previous study revealed that the injection of mAChRs antagonist scopolamine into the intermediate medial mesopallium (IMM) region, which is critical for filial imprinting, impairs memory formation. In avian brains, four mAChR subtypes have been identified (M2, M3, M4 and M5). M3 and M5 receptors increase the excitability of neurons, whereas M2 and M4 receptors reduce the excitability. Because the scopolamine blocks all subtypes, the previous study did not identify which subtype contributes to the memory formation.

④ Gene expression profiles of the muscarinic acetylcholine receptors in imprinting

Muscarinic acetylcholine receptors (mAChRs) in the central nervous system play an important role in regulating complex functions such as learning, memory, and selective attention. Five subtypes of the mAChRs (M1-M5) have been identified in mammals, and are classified into two subfamilies: excitatory (M1, M3, and M5) and inhibitory (M2 and M4) subfamilies. Filial imprinting of domestic chicks is a useful model in the laboratory to investigate the mechanisms of memory formation in early learning. We recently found that mAChRs in the intermediate medial mesopallium (IMM) are involved in the memory formation of imprinting. However, expression profiles of each mAChR subtype in the brain regions including the IMM remain unexplored.

⑤ Suppressive modulation of the forebrain network for imprinting by thyroid hormone

The thyroid hormone 3,5,3'-triiodothyronine (T_3) is considered to act acutely in the chick forebrain because focal infusion of T_3 to the intermediate medial mesopallium (IMM) causes 4 to 6-day-old hatchlings to become imprintable approximately 30 min after the infusion.

⑥ Fetal acetylcholine transmission and the biological motion in the neonatal chick.

Several environmental chemicals are suspected risk factors for autism spectrum disorder (ASD), including valproic acid (VPA) and pesticides acting on nicotinic acetylcholine receptors (nAChRs), if administered during pregnancy. However, their target processes in fetal neuro-development are unknown.

⑦ The orthologs of mammalian fear related serotonin receptor genes in the arcopallium

Fear is an adaptive emotion that elicits defensive behavioural responses against aversive threats in animals. In mammals, serotonin receptors (5-HTRs) have been shown to modulate fear-related neural circuits in the basolateral amygdala complex (BLA). To understand the phylogenetic continuity of the neural basis for fear, it is important to identify the neural circuit that processes fear in other animals. In birds, fear-related behaviours were suggested to be processed in the arcopallium/amygdala complex and modulated by the serotonin (5-HT) system. However, details about the distribution of 5-HTRs in the avian brain are very sparsely reported, and the 5-HTR that is potentially involved in fear-related behaviour has not been elucidated.

⑧ Subdivision- and layer-selective expression of serotonin receptor genes in the HF

Hippocampal formation (HF) plays a key role in cognitive and emotional processing in mammals. In HF neural circuits, serotonin receptors (5-HTRs) modulate functions related to cognition and emotion. To understand the phylogenetic continuity of the neural basis for cognition and emotion, it is important to identify the neural circuits that regulate cognitive and emotional processing in animals. In birds, HF has been shown to be related to cognitive functions and emotion-related behaviors. However, details regarding the distribution of 5-HTRs in the avian brain are very sparse, and 5-HTRs, which are potentially involved in cognitive functions and emotion-related behaviors, are poorly understood. Previously, we showed that 5-HTR1B and 5-HTR3A were expressed in chick HF.

⑨ **Serotonin receptor subfamily genes in the dopaminergic nuclei of the midbrain**

Serotonin (5-hydroxytryptamine, 5-HT) is a phylogenetically conserved modulator of numerous aspects of neural functions. Serotonergic neurons in the dorsal and median raphe nucleus provide ascending innervation to the entire forebrain and midbrain. Another important neural modulatory system exists in the midbrain, the dopaminergic system, which is associated to reward processing and motivation control. Dopaminergic neurons are distributed and clustered in the brain, classically designated as groups A8-A16. Among them, groups A8-A10 associated with reward processing and motivation control are located in the midbrain and projected to the forebrain. Recently, midbrain dopaminergic neurons were shown to be innervated by serotonergic neurons and modulated by 5-HT, with the crosstalk between serotonergic and dopaminergic systems attracting increased attention. In birds, previous studies revealed that midbrain dopaminergic neurons are located in the A8-A10 homologous clusters. However, the detailed distribution of dopaminergic neurons and the crosstalk between serotonergic and dopaminergic systems in the bird are poorly understood.

⑩ **Serotonergic neurons in the chick brainstem**

Serotonin (5-hydroxytryptamine, 5-HT) is a phylogenetically conserved modulatory neurotransmitter. In mammals, 5-HT plays an important role in the regulation of many mental states and the processing of emotions in the central nervous system. Serotonergic neurons in the central nervous system, including the dorsal raphe (DR) and median raphe (MR) nuclei, are spatially clustered in the brainstem and provide ascending innervation to the entire forebrain and midbrain. Both between and within the DR and MR, these serotonergic neurons have different cellular characteristics, developmental origin, connectivity, physiology, and related behavioral functions. Recently, an understanding of the heterogeneity of the DR and MR serotonergic neurons has been developed at the molecular level. In birds, emotion-related behavior is suggested to be modulated by the 5-HT system. However, correspondence between the raphe nuclei of birds and mammals, as well as the cellular heterogeneity in the serotonergic neurons of birds are poorly understood.

２．研究の目的、３．研究の方法、４．研究成果

① **Imprintability of newly hatched domestic chicks on an artificial object**:
A novel high time-resolution apparatus based on a running disc. *Front. Physiol.* 2022 11;13:822638. doi:10.3389/fphys.2022.822638.

We developed a novel behavioral apparatus, based on a running disc to investigate the learning processes of imprinting in newly hatched domestic chicks. In the apparatus, the chick repeatedly approached the imprinting object on the disc. The apparatus sends a transistor-transistor-logic signal every 1/10 turn of the disc to a personal computer through a data acquisition system following the chick's approach to the imprinting object on the monitor. The first process is the one in which chicks spontaneously approach the moving object. The second is an acquired process in which chicks approach an object even when it is static. In the third process, chicks discriminate between the differently colored imprinting object and the control object in the preference test. The difference in the chicks' behavior during or after the sensitive period was examined. During the sensitive period, the chicks at post hatch hour 12 and 18 developed the first imprinting training process. The chicks at post hatch hour 24 maintained learning until the second process. The chicks at post hatch hour 30 reached the discrimination process in the test. After the sensitive period, the chicks reared in darkness until post hatch day 4 exhibited poor first learning process in the training. Thus, this apparatus will be useful for the detection of behavioral changes during neuronal development and learning processes.

② **Blockade of muscarinic acetylcholine receptor by scopolamine impairs the memory formation of filial imprinting in domestic chicks (*Gallus Gallus domesticus*)**. *Behav. Brain Res.* 2020 3;379:112291. doi:10.1016/j.bbr.2019.112291.

We examined whether the imprinting acquisition in chick can be impaired by injecting mAChR antagonist scopolamine into the bilateral IMM. We show that the injection of scopolamine decreased the preference for the imprinting object in the test, but did not affect the number of approaches to the imprinting object during training. Immunoblotting and immunohistochemistry revealed that M3 receptors were expressed in the IMM. Our data suggest that acetylcholine is involved in the memory formation of imprinting through M3 receptors in the IMM.

③ **Subtype-selective contribution of muscarinic acetylcholine receptors for filial imprinting in newly-hatched domestic chicks.** *Behav. Brain Res.* 2022 29;424:113789. doi:10.1016/j.bbr.2022.113789.

By injecting several types of mAChR antagonists into the IMM, we determined which mAChR subtype plays a critical role in imprinting. Injection of the M3 antagonist (DAU5884) at 20 mM or the M5 antagonist (ML381) at 2 mM impaired imprinting. Considering the pKi value of DAU5884, the impairment seems to be caused by DAU5884 binding to M3 and/or M4 receptors. We showed that the M2 antagonist (AQ-RA741) impaired imprinting at a concentration of 20 mM. Considering the pKi value of AQ-RA741, the impairment seems to be caused by AQ-RA741 binding to M2 and/or M4. The findings suggest that the excitatory receptor subtypes M3 and M5 and the inhibitory receptor subtype M2 and/or M4 cooperate to achieve the appropriate balance of acetylcholine signaling to execute imprinting.

④ **Gene expression profiles of the muscarinic acetylcholine receptors in brain regions relating to filial imprinting of newly-hatched domestic chicks.** *Behav. Brain Res.* 2022 26;420:113708. doi:10.1016/j.bbr.2021.113708.

We showed the unique gene expression of each mAChR subtype in the pallial regions involved in imprinting. In terms of the excitatory mAChRs, M5 was expressed in the IMM region and other parts of the pallium, whereas M3 was less expressed in the IMM but highly expressed in the hyperpallium and nidopallium. Regarding the inhibitory mAChRs, M2 was sparsely distributed but clearly in some cells throughout the pallial regions. M4 was highly expressed in the IMM region and other parts of the pallium. These expression profiles can be used as a basis for understanding cholinergic modulation in the memory formation of imprinting.

⑤ **Suppressive modulation of the chick forebrain network for imprinting by thyroid hormone**: An *in vitro* study. *Front. Physiol.*2022 20; 13:881947.doi: 10.3389/fphys.2022.881947.

We examined synaptic responses of IMM neurons in slice preparations in vitro. Extracellular field potential responses to local electrical stimulation were pharmacologically dissociated to synaptic components mediated by AMPA and NMDA receptors, as well as GABA-A and -B receptors. Bath-applied T_3 (20-40 μM) enhanced the positive peak amplitude of the field potential. Bicuculline induced spontaneous epileptic bursts by NMDA receptor activation, and subsequent application of T_3 suppressed the bursting frequency. Pretreatment of slices with T_3 failed to influence the synaptic potentiation caused by tetanic stimulation. Intracellular whole-cell recording using a patch electrode confirmed the T_3 actions on the GABA-A and NMDA components. T_3 enhanced the GABA-A response and suppressed the NMDA plateau potential without changes in the resting membrane potential or the threshold of action potentials. Imprinting-associated T_3 influx may act as an acute suppressor of the IMM network.

⑥ **Fetal blockade of nicotinic acetylcholine transmission causes autism-like impairment of biological motion preference in the neonatal chick.** *Cerebral Cortex Communications*, 2022, doi.org/10.1093/texcom/tgac041

The injection of VPA into the fetus impaired imprinting to an artificial object in

neonatal chicks, while a predisposed preference for biological motion (BM) remained intact. Blockade of nAChRs acted oppositely, sparing imprinting and impairing BM preference. Beside ketamine and tubocurarine, significant effects of imidacloprid appeared at a dose ≤1 ppm. In accord with the behavioral dissociations, VPA enhanced histone acetylation in the primary cell culture of fetal telencephalon. VPA reduced the brain weight and the ratio of NeuN-positive cells (matured neurons) in the telencephalon of hatchlings. Despite the distinct underlying mechanisms, both VPA and nAChR blockade similarly impaired imprinting to biological image composed of point-light animations. Furthermore, both impairments were abolished by postnatal bumetanide treatment. Neurotransmission via nAChR is thus critical for the early social bond formation, which is hindered by ambient neonicotinoids through impaired visual predispositions for animate objects.

⑦ **The dorsal arcopallium of chicks displays the expression of orthologs of mammalian fear related serotonin receptor subfamily genes.** *Sci. Rep.* 2020 3;10(1):21183. doi:10.1038/s41598-020-78247-9

We showed that orthologs of mammalian 5-HTR genes that are expressed in the BLA, are expressed in a part of the chick arcopallium/amygdala complex called the dorsal arcopallium. This suggests that serotonergic regulation in the dorsal arcopallium may play an important role in regulating fear-related behaviour in birds. Our findings can be used as a basis for comparing the processing of fear and its serotonergic modulation in the mammalian amygdala complex and avian arcopallium/amygdala complex.

⑧ **Chick hippocampal formation displays subdivision- and layer-selective expression patterns of serotonin receptor subfamily genes.** *Front. Physiol.* 2022 8;13:882633. doi:10.3389/fphys.2022.882633.

We performed in situ hybridization in the chick telencephalon and found that 5-HTR1D, 5-HTR1E, 5-HTR5A, and 5-HTR7 were expressed in the chick HF, especially 5-HTR1D and 5-HTR1E, which showed subdivision- and layer-selective expression patterns, suggesting that the characteristic 5-HT regulation is involved in cognitive functions and emotion-related behaviors in these HF regions. These findings can facilitate the understanding of serotonin regulation in avian HF and the correspondence between the HF subdivisions of birds and mammals.

⑨ **Dopaminergic nuclei in the chick midbrain express serotonin receptor subfamily genes.** *Front. Physiol.* 2022 8;13:1030621. doi:10.3389/fphys.2022.1030621.

We prepared RNA probes for chick orthologues of dopaminergic neuron-related genes, noradrenaline-related genes, and serotonin receptor genes. We confirmed that the expression of tyrosine hydroxylase (TH) and NAT was well-matched in all chick dopaminergic nuclei examined. This supported that the compensation of the function of dopamine transporter (DAT) by NAT is a general property of avian dopaminergic neurons. Furthermore, we showed that 5-HTR1A and 5-HTR1B were expressed in midbrain dopaminergic nuclei, suggesting the serotonergic regulation of the dopaminergic system via these receptors in chicks. Our findings will help us understand the interactions between the dopaminergic and serotonergic systems in birds at the molecular level.

⑩ **Serotonergic neurons in the chick brainstem express various serotonin receptor subfamily genes.** *Front. Physiol.* 2022 17;12:815997. doi:10.3389/fphys.2021.815997.

We prepared RNA probes for chick orthologs of the following serotonin receptor genes: 5-HTR1A, 5-HTR1B, 5-HTR1D, 5-HTR1E, 5-HTR1F, 5-HTR2A, 5-HTR2B, 5-HTR2C, 5-HTR3A, 5-HTR4, 5-HTR5A, and 5-HTR7. We showed that the expression pattern of 5-HT receptors in the serotonin neurons of chick DR and MR may vary, suggesting heterogeneity among and within the serotonin neurons of the DR and MR in the chick brainstem. Our findings will facilitate a good understanding of the correspondence between bird and mammalian raphes.

５．主な発表論文等

〔雑誌論文〕　計11件（うち査読付論文　9件／うち国際共著　0件／うちオープンアクセス　7件）

１．著者名 Matsushima Toshiya、Miura Momoko、Patzke Nina、Toji Noriyuki、Wada Kazuhiro、Ogura Yukiko、Homma Koichi J、Sgad? Paola、Vallortigara Giorgio	４．巻 -
２．論文標題 Fetal blockade of nicotinic acetylcholine transmission causes autism-like impairment of biological motion preference in the neonatal chick	５．発行年 2022年
３．雑誌名 Cerebral Cortex Communications	６．最初と最後の頁 -
掲載論文のDOI（デジタルオブジェクト識別子） 10.1093/texcom/tgac041	査読の有無 有
オープンアクセス オープンアクセスとしている（また、その予定である）	国際共著 －

１．著者名 Fujita Toshiyuki、Aoki Naoya、Mori Chihiro、Serizawa Shouta、Kihara-Negishi Fumiko、Homma Koichi J.、Yamaguchi Shinji	４．巻 13
２．論文標題 Dopaminergic nuclei in the chick midbrain express serotonin receptor subfamily genes	５．発行年 2022年
３．雑誌名 Frontiers in Physiology	６．最初と最後の頁 -
掲載論文のDOI（デジタルオブジェクト識別子） 10.3389/fphys.2022.1030621	査読の有無 有
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１．著者名 Mori Chihiro、Aoki Naoya、Fujita Toshiyuki、Yamaguchi Shinji、Matsushima Toshiya、Homma Koichi J.	４．巻 420
２．論文標題 Gene expression profiles of the muscarinic acetylcholine receptors in brain regions relating to filial imprinting of newly-hatched domestic chicks	５．発行年 2022年
３．雑誌名 Behavioural Brain Research	６．最初と最後の頁 113708～113708
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１．著者名 Aoki Naoya、Mori Chihiro、Fujita Toshiyuki、Serizawa Shouta、Yamaguchi Shinji、Matsushima Toshiya、Homma Koichi J.	４．巻 424
２．論文標題 Subtype-selective contribution of muscarinic acetylcholine receptors for filial imprinting in newly-hatched domestic chicks	５．発行年 2022年
３．雑誌名 Behavioural Brain Research	６．最初と最後の頁 113789～113789
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1．著者名 Saheki Yuriko、Aoki Naoya、Homma Koichi J.、Matsushima Toshiya	4．巻 13
2．論文標題 Suppressive Modulation of the Chick Forebrain Network for Imprinting by Thyroid Hormone: An in Vitro Study	5．発行年 2022年
3．雑誌名 Frontiers in Physiology	6．最初と最後の頁 -
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1．著者名 Fujita Toshiyuki、Aoki Naoya、Mori Chihiro、Fujita Eiko、Matsushima Toshiya、Homma Koichi J.、Yamaguchi Shinji	4．巻 13
2．論文標題 Chick Hippocampal Formation Displays Subdivision- and Layer-Selective Expression Patterns of Serotonin Receptor Subfamily Genes	5．発行年 2022年
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1．著者名 Aoki Naoya、Mori Chihiro、Fujita Toshiyuki、Serizawa Shouta、Yamaguchi Shinji、Matsushima Toshiya、Homma Koichi J.	4．巻 13
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1．著者名 Naoya Aoki, Toshiyuki Fujita, Chihiro Mori, Eiko Fujita, Shinji Yamaguchi, Toshiya Matsushima, Koichi J Homma	4．巻 379
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3．雑誌名 Behavioural brain research	6．最初と最後の頁 112291
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1．著者名 Toshiyuki Fujita, Naoya Aoki, Chihiro Mori, Eiko Fujita, Toshiya Matsushima, Koichi J Homma, Shinji Yamaguchi	4．巻 10(1)
2．論文標題 The dorsal arcopallium of chicks displays the expression of orthologs of mammalian fear related serotonin receptor subfamily genes.	5．発行年 2020年
3．雑誌名 Scientific reports	6．最初と最後の頁 21183
掲載論文のDOI（デジタルオブジェクト識別子） 10.1038/s41598-019-56960-4	査読の有無 有
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1．著者名 Serizawa Shouta、Aoki Naoya、Mori Chihiro、Fujita Toshiyuki、Yamaguchi Shinji、Matsushima Toshiya、Homma Koichi J.	4．巻 14
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3．雑誌名 Frontiers in Physiology	6．最初と最後の頁 -
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1．著者名 Fujita Toshiyuki、Aoki Naoya、Mori Chihiro、Fujita Eiko、Matsushima Toshiya、Homma Koichi J.、Yamaguchi Shinji	4．巻 12
2．論文標題 Serotonergic Neurons in the Chick Brainstem Express Various Serotonin Receptor Subfamily Genes	5．発行年 2022年
3．雑誌名 Frontiers in Physiology	6．最初と最後の頁 -
掲載論文のDOI（デジタルオブジェクト識別子） 10.3389/fphys.2021.815997	査読の有無 無
オープンアクセス オープンアクセスではない、又はオープンアクセスが困難	国際共著 －

〔学会発表〕　計11件（うち招待講演　1件／うち国際学会　1件）

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〔図書〕　計0件

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６．研究組織

	氏名 （ローマ字氏名） （研究者番号）	所属研究機関・部局・職 （機関番号）	備考

７．科研費を使用して開催した国際研究集会

〔国際研究集会〕　計0件

８．本研究に関連して実施した国際共同研究の実施状況

共同研究相手国	相手方研究機関