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博士論文の要旨

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論文題目 Social biases affecting self–other matching in Japanese macaques
(ニホンザルにおける自他の状態マッチングの社会的影響要因)

A phenomenon in which a state of one individual triggers a congruent state in another is called “self–other matching.” For group-living animals, the capacity to match one’s states with those of conspecifics is advantageous for survival and reproductive success. Studying the mechanisms of self–other matching will provide some insights into how animals cope with the problems they face in group life. Some classical studies assumed that self–other matching is based on a reflex-like response. However, recent studies have shown that the likelihood of self–other matching is not equal among all individuals but is affected by social biases. These studies suggested that self–other matching involves not only a reflex-like mechanism but also more complex mechanisms that are regulated by social context.

In this thesis, I addressed the following three issues raised in previous studies. First, previous researches on social biases in behavioral matching focused primarily on positively valenced behaviors (e.g., play signals) and ones with neutral valence (e.g., yawning). However, little research has been done on negatively valenced behaviors. The way in which individuals act on the emotional states of others may depend on the type of emotional valence of the behavior. Hence, there is a good reason to believe that the effects of social biases on contagious matching vary with the valence of the behavior. The second problem with previous studies is that they have exclusively focused on the matching of an instant, event-like behavior such as yawning. Some types of self–other matching can be maintained over time. Social biases on the maintained self–other matching remain unknown. Third, individuals sometimes fail to maintain self–other matching. Social play provides a clear example of the failure of matching. In some rare cases, previously shared playful states can dissociate, and playful interaction escalates into overt conflict. Studying factors associated with the failure of self–other matching can illuminate the mechanisms of successful matching from a different angle. However, social biases affecting the failure of maintenance of self–other matching remain largely unknown. I addressed these issues by using data of vigilance and play fighting in a group of Japanese macaques.

In the first study (Chapter 2), I examined social biases in the contagion of vigilance, which is considered an emotionally negative behavior. Studies have shown that several social factors (e.g., familiarity, dominance, the mother–offspring relationship) affect behavioral contagion. Our findings revealed that vigilance

exhibited by a given individual was more contagious to lower-ranked than to higher-ranked individuals. In addition, vigilance was more contagious to mothers from their offspring than vice versa. Thus, the susceptibility to vigilance exhibited by others varies according to the social status of each individual and the relationship between each pair of individuals. By contrast, we did not find any effects of kinship on vigilance contagion. This implies that familiarity bias, which is often reported to be associated with the contagion of yawning and play signals, does not influence vigilance contagion. Overall, our findings indicate that social bias may not affect all types of contagious matching in the same way, but rather contagious matching is affected by the interplay of the adaptive meaning of behavior and social biases.

In the second study (Chapter 3), I focused on play fighting and examined the relationship between the maintenance of shared playful state and facial signal (i.e., play face). I found that male juveniles were more likely than females to express play face before initiating play with other males and that juveniles were more likely to express play face before playing with others closer in age. Considering that Japanese macaque males have stronger motivation to play than females and that juveniles prefer to play with individuals of the same age, play face before play initiation may reflect the individual's motivation for the interaction that is about to start. The observation that play bouts preceded by play face lasted longer than those not preceded by play face supports this interpretation. Also, we found that the expression of play face by an individual before play prolonged the time during which the partner attacked the expresser unilaterally. This implies that receivers of play face might be able to deliver playful attacks more vigorously. Overall, our results indicate that play face expression before play initiation functions to display the expresser's play motivation and maintain a shared state over a period by promoting active engagement of the recipients.

In the third study (Chapter 4), I examined social factors affecting the failure of maintenance of playful state matching. When play escalated, I defined the individual expressing negative responses (e.g., screaming and bared-teeth displays) as the "victim" and the other individual as the "aggressor." I found that individuals with a lower social rank than their playmates were more likely to be victims in escalations in same-age dyads. Furthermore, individuals that were younger and smaller than their playmates were more likely to be victims in escalations in mixed-age dyads. These results suggested that inter-individual differences determined by dominance relationships and developmental stages affect how self-other matching breaks down. In addition, I found that individuals that subsequently became aggressors had maintained an advantage for a longer duration during the preceding bout of play fighting compared to individuals that became victims. The results imply that escalation might have occurred because one individual (i.e., a higher-ranked or older individual) held an excessive advantage, and play lost its reciprocity. Overall, our results suggested that inter-individual differences may have led to asymmetries in play interactions, and these asymmetries

may have caused the failure of maintenance of shared playful states.

In conclusion, this thesis suggests that self–other matching should be viewed as a more complex process than has been assumed by previous studies. Prior studies have focused primarily only on whether instant state matching occurs, with little attention to the adaptive meaning that varies from behavior to behavior and the time range of matching. The overlap between oneself and others is not simply determined by emotional closeness and social contexts. Instead, the overlap will depend on which behavioral and emotional states the researcher focuses on, each with a different adaptive meaning. Also, the self–other overlap can change over time: interactants manage their state matching with signals, and sometimes state dissociation occurs. In addition, ecological and social conditions, which vary from species to species, may affect patterns of self–other matching. A comparative study that takes into account the complex nature of self–other matching suggested by this thesis is expected to shed further light on the evolutionary background of basic social cognitive skills.

博士論文審査結果

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Title
論文題目 Social biases affecting self-other matching in Japanese macaques

出願者は、野生ニホンザルを対象に、行動や情動状態を他個体と一致させる現象 (self-other matching; 以下、SOM と略記) を研究した。第 1 章では、SOM に関するこれまでの研究が概説されている。特に、SOM の生起には社会的要因 (social bias) の影響が重要であるが、これまでの研究では統一的な見解が得られていないことが述べられている。また、これまでに行われてきた多くの研究は、短時間で終わる行動に関する SOM を対象としていたが、比較的長時間継続する行動状態に関する SOM に関する研究は進んでいないことが指摘されている。これらの問題点に基づき、本博士論文における三つの研究の意義づけがなされている。

第 2 章では、野生ニホンザルにおける視覚的警戒行動(vigilance behaviour)にみられる行動伝染を報告している。順位関係が専制的で血縁関係が重要なニホンザル社会の特性を踏まえて、群れ内の順位関係および血縁関係が行動伝染の生起に影響すると予測した。餌場にいる二個体を対象に行動観察を行い、個体間の血縁関係、相対的順位関係、個体の群内順位などの社会的要因が、視覚的警戒行動の同調に与える影響を調べた。その結果、視覚的警戒行動は絶対的順位が劣位である個体に対して、優位な個体に対してよりも高確率で伝染していた。また、視覚的警戒行動の伝染は、母親から未成年体に対してよりも、未成年体から母親に対して高確率で起きていた。これらの結果は、視覚的警戒行動という負の情動を伴う行動の SOM を扱ったという点で希有な研究である。本章の結果は *Animal Behaviour* 誌に掲載されている。

第 3 章では、SOM が長時間継続する闘争遊び(play fighting)を対象とし、遊びに関連して表出される特有の表情(play face)の機能を調べた。特に、遊びの開始前に表出される play face が、発信個体の遊びに対する積極性を示しているという仮説を検証するために、表出の決定要因、および play face がその後の遊びの継続時間に与える影響が調べられた。その結果、play face は遊び頻度が高い個体間 (オス同士、同年齢個体同士) の遊びにおいて頻繁に表出されていた。また、play face が発出されて始まった遊びは、そうでない遊びと比較して、長い時間継続した。これらの結果は、play face が表出個体の積極性を示し、遊びを維持するための信号となっていることを示している。遊びの途中で表出される play face を扱う従来の研究と比べて、本研究は遊び開始時の play face に着目した点で独自性が高く、SOM が維持されるメカニズムに関する新たな知見をもたらしたと評価できる。

第 4 章では、闘争遊びが攻撃交渉に発展するという SOM が破綻する状況に焦点を当て、遊びを破綻させた個体の特性とその行動役割を検証した。とくに、二個体間の非対称性が、闘争遊びの破綻の原因となる可能性に着目し、相対的順位が高い、または年齢が相対的に高い個体が遊びを破綻させるという予測を検証している。結果はこの二つの予測を支持す

るものであった。また、闘争遊びを破綻させた個体は、それ以前に、闘争遊びのなかで優勢な役割を果たしていたことも明らかにした。本研究は、闘争遊びが破綻するという希少な事例を丹念に集め、その決定要因と行動学的原因を解明したものであり、高い学問的価値を持つ。

総合考察にあたる第5章では、三つの研究に基づき、**SOM**のメカニズムに関する新たな枠組みを提案している。また、未解明な点、今後の展望が簡潔に述べられている。

本博士論文は、**SOM**に関する新たな知見が多く含まれており、包括的な理解を目的とする新たな枠組みを提案する意欲的な博士論文となっている。これらの点から、学術的価値が極めて高いと評価した。以上の理由により、審査委員会は、本論文が学位の授与に値すると判断した。