UNIVERSITÉ PARIS 13

École doctorale **Galilée**
Unité de recherche **Laboratoire d'Éthologie Expérimentale et Comparée**

Thèse présentée par **Tatiana FORESTIER**
Soutenue le **8 mars 2018**
En vue de l'obtention du grade de docteur de l'Université Paris 13

Discipline **Éthologie**

Titre de la thèse

Environnement socio-olfactif et choix alimentaires chez la souris domestique, *Mus musculus domesticus*

Thèse dirigée par Patrick GOUAT
Christophe FÉRON

Composition du jury

Président du jury	Heiko G. RÖDEL	professeur au LEEC, Université Paris 13
Rapporteurs	Elena CHOLERIS	professeure à l'University of Guelph
	Matthieu KELLER	directeur de recherche au CNRS/INRA, Université de Tours
Examinateurs	Gérard COUREAUD	chargé de recherche HDR au CNRS/CRNL, Université Lyon 1
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Directeurs de thèse	Patrick GOUAT	MCF HDR au LEEC, Université Paris 13
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Université Paris 13

Doctoral School **Galilée**
University Department **Laboratoire d’Éthologie Expérimentale et Comparée**

Thesis defended by **Tatiana Forestier**
Defended on **8th March, 2018**
In order to become Doctor from Université Paris 13
Academic Field **Ethology**

Thesis Title

Socio-olfactory world and food selection in the house mouse, *Mus musculus domesticus*

Thesis supervised by Patrick Gouat
Christophe Féron

Committee members

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Mots clés : apprentissage social, attention, perception olfactive, rongeurs

Keywords: attention, olfactory perception, rodents, social learning

Cette thèse a été préparée au

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À Gisèle Roman,

Notre plus grande gloire n’est pas de ne jamais tomber, mais de nous relever après chaque chute.

Confucius

ENVIRONNEMENT SOCIO-OLFACTIF ET CHOIX ALIMENTAIRES CHEZ LA SOURIS DOMESTIQUE, *Mus musculus domesticus*

Résumé

Le succès écologique de la souris domestique, *Mus musculus domesticus*, repose en partie par sa capacité à adapter son régime alimentaire aux ressources disponibles. La transmission sociale des préférences alimentaires (TSPA) est un apprentissage observé chez les rongeurs, leur permettant d'élargir leur répertoire alimentaire à moindre risque en obtenant des informations olfactives sur de nouveaux aliments à partir des congénères. Cet apprentissage social s'observe directement, lors d'une rencontre avec un congénère ou indirectement, via des marques odorantes. Ce travail a pour but de déterminer comment les souris utilisent leur environnement socio-olfactif pour réaliser des choix alimentaires. Nos résultats ont révélé que l'absence du congénère lors de la TSPA indirecte réduit les contraintes sociales associées à une rencontre et permet l'acquisition de la TSPA entre femelles inconnues. Cependant, certaines contraintes physiques associées à la perception des informations dans les fèces peuvent réduire la disponibilité des informations alimentaires. Enfin, nous avons montré que les différentes préoccupations sexuelles des individus affectent la hiérarchisation des informations présentes dans les fèces et limitent, chez les mâles, l'acquisition de la TSPA. Nos résultats suggèrent que l'utilisation d'informations alimentaires chez les souris varie selon leur contexte social et écologique et implique différents processus tels que l'émotion et l'attention. En conditions naturelles, les voies directe et indirecte de la TSPA pourraient être complémentaires, chacune élargissant les conditions de transmission de l'information alimentaire chez les rongeurs.

Mots clés : apprentissage social, attention, perception olfactive, rongeurs

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SOCIO-OLFACTORY WORLD AND FOOD SELECTION IN THE HOUSE MOUSE, *Mus musculus domesticus*

Abstract

The ecological success of the house mouse, *Mus musculus domesticus*, implies a great capacity to adapt its diet to available food resources. The social transmission of food preference (STFP) is an adaptive type of learning observed in rodents allowing them to enlarge their food repertoire at lower risk by getting olfactory information on novel food sources from conspecifics. This social learning takes place directly, during an encounter with a conspecific or indirectly, via olfactory marks. The objective of this thesis work was to determine how mice use their socio-olfactory environment to make food choices. Our results revealed that the absence of the conspecific during the indirect STFP reduces the social constraints associated with an encounter and allows the acquisition of STFP between unfamiliar conspecifics. However, some physical constraints associated with the perception of information in feces may reduce the availability of food information. We also showed that different sex concerns of individuals may affect the prioritization of information present in feces and limit, in males, the acquisition of STFP. Our results suggest that the use of food information in mice varies according to their social and ecological context and involves different processes such as emotion and attention. Under natural conditions, the direct and indirect STFP could be complementary, each of them extending the conditions for the transmission of food information in rodents.

Keywords: attention, olfactory perception, rodents, social learning

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Remerciements - Acknowledgments

Acknowledgments to the Jury members

First of all, I would like to express my heartfelt thanks to each member of the Jury for accepting my invitation to take part in my thesis defense and evaluating my thesis work : Prof. Heiko G. Rödel, Prof. Elena Choleris, Dr. Matthieu Keller, Dr. Gérard Coureaud, Dr. Virginie Lattard, Dr. Christophe Féron and Dr. Patrick Gouat.

Special thanks to Dr. Gérard Coureaud for following the evolution of this thesis and for the wise advice he has given me.

I would like to thank Prof. Heiko G. Rödel for his discreet attention to his doctoral students, for his support and invaluable help during my thesis. I think I was very lucky to work in a laboratory that has a director with both such scientific and human qualities, thank you very much.

Remerciements

Je souhaiterais également remercier M. Denis Bitouzé, qui a offert aux doctorants de l'Université Paris 13 une formation LaTeX d'une très grande qualité et qui m'a donné les outils nécessaires pour produire ce manuscrit de thèse. Merci pour votre grande pédagogie.

...aux relecteurs du manuscrit

Je tiens à exprimer ma profonde gratitude à M. Abdessattar Belaouaid pour avoir révisé, malgré de brefs délais, l'anglais de l'introduction de mon manuscrit de thèse.

Merci également au Dr. Gilles Gheusi pour avoir révisé le contenu scientifique de plusieurs parties de ce manuscrit.

...à mes collaborateurs

Je tiens à remercier le Prof. Patrizia d'Ettorre et Chloé Leroy pour le travail de collaboration qu'elles ont fourni tout au long de cette thèse et pour leurs précieux conseils sur les analyses chimiques.

Je remercie également les partenaires industriels du projet NEORAMUS : la SAS Liphatech, la société midi-pyrénéenne AB7 Innovation ainsi que l'école VetAgroSup de Lyon pour les projets de collaboration qui ont été mis en place dans le cadre de cette thèse et le matériel fourni qui a contribué à la réalisation de mes expériences.

...à mes directeurs de thèse

Un manuscrit de thèse entier ne serait pas suffisant pour exprimer toute ma gratitude à mes deux directeurs de thèse, Dr. Christophe Féron et Dr. Patrick Gouat. Cependant, puisque j'en ai l'occasion, je tiens tout de même à vous remercier chaleureusement pour ces années de thèse passées ensemble et pour toute la souffrance que vous ne m'avez (presque) pas faite endurer. Merci de m'avoir fait grandir scientifiquement et humainement. La thèse est une sacrée aventure qui, je pense, ne peut être vécue passionnément que lorsqu'on a des directeurs de thèse de qualité. Je vous remercie tous les deux pour m'avoir embrouillé l'esprit plus d'une fois parce que vous n'aviez pas toujours le même avis et m'avoir ainsi montré que différents points de vue présentant chacun de solides arguments scientifiques pouvaient répondre à une seule et même question.

Merci Christophe pour ton soutien tout au long de cette thèse et pour tes remarques toujours très pertinentes. Tu as été bien des fois l'élément qui nous (Patrick et moi) a ramenés sur la terre ferme. J'ai eu beaucoup de plaisir à travailler avec toi, tes qualités en tant que scientifique ont été un atout essentiel au déroulement de cette thèse et je te remercie très sincèrement pour m'avoir accompagnée tout au long de cette thèse et de m'avoir (presque) supportée tous les jours.

Merci Patrick pour avoir toujours cru en moi et pour m'avoir épaulée comme tu l'as fait. C'est toi qui m'a offert l'opportunité de réaliser cette thèse et je suis très fière d'être ta doctorante. Pour reprendre ton affectueuse expression, tu as "porté ta croix" jusqu'au bout et avec beaucoup de brio et pour cela je t'en suis extrêmement reconnaissante. Merci pour tes qualités scientifiques et tes corrections incompréhensibles avec tes jeux de mots datant de l'âge de pierre. En plus de m'avoir apporté une formation scientifique d'une très grande qualité, tu m'as montré que rigueur et sérieux pouvaient aller de pair avec humour, empathie et attention. J'ai été plus que ravie de partager cette aventure avec toi.

...à toute l'équipe du LEEC

Je remercie tous les membres de l'équipe du LEEC pour leurs discussions scientifiques, leur précieuse aide, leur soutien et pour l'ambiance de travail qu'ils créent au laboratoire, car réaliser une thèse dans des conditions sociales aussi excellentes est un élément essentiel à sa réussite.

Un grand merci à Leila Karrout pour ton sourire de tous les jours, ta précieuse aide administrative et pour les échanges toujours agréables que nous avons eu ensemble.

Merci à Alain Le Négrate pour ton aide technique et pour nos échanges agréables.

Merci à Stéphane Chameron, Renée Fénéron, Elise Nowbahari, Jean-Luc Durand, Cécile Boyer (chercheur associé au LEEC) et Claudio Carere (chercheur associé au LEEC) pour l'attention que vous m'avez exprimée durant mon séjour au laboratoire et pour les échanges passionnants que nous avons eus.

Je tiens à remercier mes voisins de bureau, Fabrice Savarit et Chantal Poteaux-Léonard pour m'avoir si gentiment accueillie dans votre bureau et offert de très bonnes conditions de travail. Fabrice, merci pour toutes nos discussions et pour ta précieuse aide lorsque j'exprimais mes tracas de doctorante. Chantal, merci pour nos discussions et pour m'avoir fait découvrir les joies de la médiation scientifique (et ce n'est pas ironique).

Je tiens à remercier Paul Devienne, Nicolas Pineros Cuellar (ingénieur pédagogique et designer du Fablab de l'Université paris 13) et Sébastien Augen (membre bénévole du Fablab de l'Université paris 13) pour les idées de génie et le temps précieux qu'ils m'ont accordé pour l'élaboration de mes dispositifs.

Je remercie Gilles Gheusi pour la bonne humeur que tu apportes au laboratoire et pour les échanges que nous avons eus durant ces années notamment dans le cadre du monitorat. Bien que ce ne soit pas toujours évident de travailler en équipe, j'ai été ravie de travailler avec toi et Fabrice en CPO et NSC.

Merci à David Sillam-Dussès pour ta bienveillance depuis le master et pour m'avoir toujours donné de précieux conseils. C'est un plaisir de discuter avec toi et de relever les défis que tu me confies (tu noteras que toutes les pièces sont parvenues à son destinataire avant la fin de mon doctorat, mission accomplie).

Merci à Maria Cristina Lorenzi pour ton attention et ton touchant soutien durant ces années de thèse. Ce fut une vraie joie de te rencontrer et de converser avec toi, j'espère avoir de nouveau l'occasion de "grignoter" (avec ce génial accent italien) avec toi lors d'un prochain congrès.

Un grand merci à Ludivine Jaravel, responsable animalière du LEEC (mais aussi officieusement psychologue des doctorants et coiffeuse professionnelle de souris) qui m'a suivie tout au long de cette thèse et dont la coopération dans le travail et l'amitié ont rendu les manips tellement plus simples.

...aux étudiants

Je remercie tous les étudiants que j'ai eu la chance de rencontrer à l'Université durant mes années de thèse. Grâce à nos discussions et nos partages d'angoisses, vous avez grandement contribué au développement de mes idées et à la construction de mes raisonnements scientifiques au cours de cette thèse. Un merci particulier à Lluis Socias, Matilde Sauvaget, Marylin Rangassamy, Laura Picchi, Benoit Baudrillart, Isabella Clegg, Adeline Fourdan, Thomas Raveleau, Romain Barreteau, Aurélie Verjat.

Je tiens également à remercier plus particulièrement les stagiaires qui ont participé à ce projet de thèse et qui se sont pleinement investis dans leurs stages : Thomas Raveleau, Roxanne Sabatier, Adélia Delouche et Ania Oukid.

...à mes proches

Je tiens à remercier tous mes proches pour m'avoir supportée ou au contraire pour avoir supporté ma désertion durant ces années intenses de thèse.

Évidemment, merci à toute la bande du LEEC (Ludi, Célichou, DJ Daph, Aurélie CPM, Miss Italie, Roxy, Romain, Thomas, Mary) pour nos soirées endiablées carnaval, bal masqué, olé olé etc. (je crée des rumeurs pour les étudiants ;)). Non plus sérieusement merci à vous pour nos soirées rami chaque vendredi ça m'a beaucoup aidée... ;) Merci pour votre présence tout au long de cette thèse, pour vos personnalités exceptionnelles et pour tous nos délires incompréhensibles pour le commun des mortels mais qui ont été des bouffées d'oxygène à chaque instant (au point d'avoir mal aux zygomatiques à force de rire).

Merci à mes chéries Aurélie Guion et Julianne Nivelle ainsi qu'à mon frérot Franklin Forestier pour m'avoir épaulée durant cette thèse et m'avoir accueillie chez vous lorsque la coupe commençait à être pleine. Merci de m'avoir offert quelques rayons de votre soleil du sud qui me manquait cruellement ;)

Merci à Jacky et Coco, pour votre présence, vous avez été comme des arrière-arrière-arrière grands-parents pour moi (humour), vous faites tous les deux de supers parrain et marraine de coeur et j'ai eu vraiment beaucoup de joie à vous avoir à mes côtés durant ces années de thèse. Merci pour vos attentions, elles me vont droit au coeur.

Je remercie grandement toute ma famille de sang et de coeur et particulièrement mes parents, mes frères et ma soeur pour avoir toujours cru en moi et pour m'avoir constamment soutenue dans mes choix/rêves (même les plus fous). Merci à ma maman pour les conseils avisés dont tu as toujours su faire preuve et pour ta présence (même à des milliers de kilomètres) chaque fois que j'en ai eu besoin. Tout ça, c'est grâce à toi.

Je remercie particulièrement ma grand-mère de coeur qui n'aura pas eu l’occasion de voir ce travail finalisé mais qui a toujours beaucoup cru en moi. Bien que je n’ai jamais été très claire pour lui expliquer les tenants et les aboutissants de cette thèse, elle a été un moteur à bien des moments et j’aurais aimé la rendre fière.

Enfin, "The last but not the least", merci à ma moitié pour son incroyable soutien depuis le commencement de cette thèse jusqu’à sa finalité. Merci d’avoir accepté (malgré toi) ce troisième élément dans notre vie et pour l’infinie patience dont tu as fait preuve avec moi et mes autres mini-moi. Je promets (d’essayer) d’être moins terrible pour la prochaine année à venir, pour les autres on verra ;)

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Résumé substantiel

Diversifier ses sources d'approvisionnement est une des clefs de la survie d'un individu et de ses capacités d'adaptation aux changements du milieu. Une espèce ubiquiste comme la souris domestique, *Mus musculus domesticus*, est capable de coloniser des milieux très différents de son milieu naturel d'origine et est ainsi considérée comme une spécialiste de la non-spécialisation [1]. Elle a suivi l'être humain dans ses déplacements et est présente presque partout sur Terre. Cette réussite écologique implique des adaptations drastiques du régime alimentaire afin d'utiliser au mieux les ressources disponibles localement. Inclure de nouveaux aliments dans son régime alimentaire constitue néanmoins un risque pour l'individu. Que ce soit en milieu naturel ou en milieu anthropisé, les risques d'intoxication sont nombreux. Afin de réduire les coûts associés à ces risques, les souris peuvent utiliser les congénères comme sources d'information. Cette aptitude à utiliser une telle information sociale a été montrée chez diverses espèces de rongeurs et a été particulièrement bien étudiée chez le rat, *Rattus norvegicus* [2]. Une interaction sociale entre un individu dit démonstrateur qui a exploité une source alimentaire nouvelle et un congénère naïf, appelé observateur, aboutira à lever la néophobie de ce dernier qui consommera plus facilement ce nouvel aliment. Cet apprentissage social, appelé *transmission sociale des préférences alimentaires* (TSPA) permet potentiellement aux individus d'augmenter la diversité de leurs ressources alimentaires à moindre risque.

L'implication d'indices olfactifs a été mise en évidence dans ce mécanisme d'apprentissage. Il apparait que les informations odorantes véhiculées par les traces alimentaires portées par le démonstrateur, ne prennent de valeur que

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[1] Morris, D. (1967). *The Naked Ape : A zoologist's study of the human animal* (McGraw-Hill Book Company, Ed.).

[2] reviewed by Galef, B. G. (2012). A case study in behavioral analysis, synthesis and attention to detail : Social learning of food preferences. *Behavioural Brain Research*, *231*, 266–271.

si elles prennent place au sein d'une interaction sociale. Toutefois, la présence d'un rat démonstrateur anesthésié, ayant consommé auparavant un aliment nouveau, est suffisante pour faciliter la consommation de ce même type de nourriture chez les observateurs. Ainsi, la présence simultanée d'une odeur de congénère et d'une odeur alimentaire est nécessaire pour induire la TSPA mais les comportements exprimés par le démonstrateur lors de l'interaction ne sont pas décisifs. Cette acquisition implique le disulfure de carbone, une molécule exhalée par le démonstrateur, dont les mécanismes neurobiologiques sous-jacents ont été décrits dans le détail [3]. Les récepteurs répondant au disulfure de carbone répondent également à l'uroguanyline, un peptide présent dans l'urine et les fèces des rongeurs. L'uroguanyline peut agir comme un stimulus social de la même manière que le disulfure de carbone et favoriser la TSPA chez la souris [4]. Ce processus n'implique pas un contact direct entre l'observateur et le donneur d'odeur. On parle alors de TSPA indirecte par comparaison avec la TSPA directe décrite précédemment.

De nombreuses études chez des animaux de laboratoire ont permis de comprendre les mécanismes majeurs de cette influence sociale et la robustesse de la TSPA directe chez les rongeurs. Cependant, peu d'études ont porté sur les conditions fonctionnelles dans lesquelles la TSPA pourrait être efficace, notamment dans le cas de la voie indirecte. Les odeurs corporelles constituent une source fiable et largement utilisée par les congénères. Elles renseignent autant sur les traits de l'individu (identité, proximité génétique) que sur son état (régime alimentaire, état sexuel, état de santé). Ces différentes informations bien que véhiculées par un même support semblent perçues indépendamment les unes des autres par les souris [5]. Ces caractéristiques spécifiques à la TSPA indirecte pourraient alors jouer un rôle clé dans les conditions d'acquisition de cet apprentissage. Le présent projet a pour but de déterminer comment les souris utilisent leur environnement socio-olfactif pour réaliser des choix alimentaires. En utilisant un modèle de souris d'origine sauvage, nous avons essayé de mieux

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[3] Munger, S. D. et al. (2010). An olfactory subsystem that detects carbon disulfide and mediates food-related social learning. *Current Biology*, *20*, 1438–1444.

[4] Arakawa, H. et al. (2013). The receptor Guanylyl Cyclase type D (GC-D) ligand uroguanylin promotes the acquisition of food preferences in mice. *Chemical Senses*, *38*, 391–397.

[5] Colombelli-Négrel, D. & Gouat, P. (2006). Male and female mound-building mice, *Mus spicilegus*, discriminate dietary and individual odours of conspecifics. *Animal Behaviour*, *72*, 577–583.

comprendre les conditions dans lesquelles la TSPA directe et indirecte pourraient être utilisées par les souris.

La souris domestique est un modèle d'étude particulièrement adapté à ce projet dans la mesure où ses caractéristiques facilitent l'exposition à de nouveaux items alimentaires potentiellement dangereux. En conditions naturelles, les souris domestiques forment des groupes sociaux, généralement constitués de mâles territoriaux associés à des femelles souvent apparentées qui coopèrent pour l'élevage des jeunes. Les mâles et les femelles défendent leur territoire contre les intrus du même sexe, voisins et étrangers, mais en général, le nombre d'agressions impliquant des femelles est plus faible que celles entre mâles. Les liens sociaux sont faibles entre mâles et femelles et la multiplicité des partenaires de reproduction est la règle chez cette espèce [6].

Afin de vérifier la mise en place de la TSPA en conditions de laboratoire, nous avons utilisé un paradigme général basé sur les différentes procédures développées chez le rat et la souris [7]. La procédure comprend une phase sociale suivie d'un test de choix entre deux nouveaux aliments. Durant la phase sociale, deux situations ont été testées : dans le premier cas, un observateur naïf est confronté à des informations sociales sur l'un des deux aliments par une rencontre directe avec un démonstrateur (TSPA directe) ; dans le deuxième cas, l'observateur reçoit des informations sociales à partir de marques odorantes (dépôts anogénitaux ou fèces) d'un donneur (TSPA indirecte). Chaque situation comprend deux groupes expérimentaux qui diffèrent par la nature de l'aliment expérimenté par le démonstrateur/donneur. La TSPA est considérée comme acquise lorsque les deux groupes diffèrent significativement dans leur consommation des deux aliments proposés. Afin d'atténuer l'effet de préférences intrinsèques pour un des deux aliments, l'acquisition de la TSPA a été évaluée en mesurant, pour chaque groupe expérimental, la proportion de consommation d'un des deux aliments. Cette proportion correspond à $A/(A+B)$ où A représente la quantité consommée pour le premier aliment et B représente la quantité consommée pour le second aliment, et ce quel que soit l'aliment du démonstrateur/donneur.

Dans un premier temps, nous nous sommes demandés si les contraintes so-

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[6] reviewed by König, B. & Lindholm, A. K. (2012). Evolution of the house mouse. In M. Malochán, S. J. E. Baird, P. Munclinger, & J. Piálek (Eds.), (Chap. The complex social environment of female house mice (*Mus domesticus*, pp. 114–134)). Cambridge University Press.

[7] Valsecchi, P. & Galef, B. G. (1989). Social influences on the food preferences of house mice (*Mus musculus*). *International Journal of Comparative Psychology*, *2*, 245–256.

ciales observées chez la souris domestique pouvaient affecter l'acquisition de la TSPA directe et indirecte. En conditions naturelles, compte tenu de leur organisation sociale, les souris sont supposées échanger des informations principalement au sein de leur groupe social. Cependant, étant donné que les différentes ressources alimentaires ne sont pas distribuées au hasard dans l'espace, les souris d'un même groupe partagent généralement les mêmes sources de nourriture tandis que les souris de différents groupes sociaux diffèrent davantage dans la diversification de leurs régimes alimentaires. Par conséquent, la collecte d'informations sur les aliments consommés par des congénères inconnus pourrait aider à élargir le répertoire alimentaire des individus. Cependant, l'intolérance sociale entre deux individus inconnus constitue une réelle contrainte. L'une des principales différences entre la TSPA directe et la TSPA indirecte est la présence ou l'absence du congénère lors de l'acquisition de l'information. Cette différence pourrait jouer un rôle majeur dans l'acquisition d'informations auprès de congénères inconnus. Pour évaluer l'effet de cette contrainte sociale, nous avons testé l'acquisition de la TSPA chez des souris femelles après une rencontre directe avec une femelle familière et non familière, et après la présentation des marques odorantes (dépôts anogénitaux) d'une femelle non familière. Contrairement aux rencontres entre femelles familières, nos résultats ne fournissent pas d'argument significatif à l'existence d'une TSPA après des rencontres entre deux femelles non familières. En revanche, une TSPA est clairement mise en évidence chez des femelles ayant flairé les marques odorantes de femelles non familières. Ces résultats suggèrent que l'altération de la TSPA directe pourrait être liée à un contexte stressant induit par la présence d'un congénère non familier. En effet, plusieurs études ont montré que le stress pouvait affecter les processus d'apprentissage et de mémoire, notamment dans le cadre de la TSPA [8]. De plus, l'efficacité de la TSPA indirecte entre femelles non familières laisse supposer que l'altération de la TSPA directe n'est pas une conséquence de l'origine de l'information sociale (un potentiel compétiteur) mais semble davantage affectée par le contexte induit par l'interaction sociale. De ce fait, contrairement à une rencontre directe, les marques odorantes des congénères inconnus semblent être un moyen moins coûteux pour les souris, en termes de contraintes sociales, pour accéder à des informations sur de nouvelles ressources alimentaires.

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[8] van der Kooij, M. A. & Sandi, C. (2012). Social memories in rodents : Methods, mechanisms and modulation by stress. *Neuroscience and Biobehavioral Reviews*, *36*, 1763–1772.

Une autre différence qui existe entre ces deux voies de TSPA réside dans l'information recueillie sur l'aliment par les souris. Dans le cas de la TSPA directe, l'odeur du nouvel aliment provient de l'haleine ou des restes de nourriture présents sur le congénère et ne devrait pas différer de son odeur initiale. La TSPA indirecte, en revanche, implique une transformation des caractéristiques de l'aliment par le système digestif qui peut altérer les informations initiales liées à l'odeur de l'aliment. Dans ce cas, certains marqueurs odorants peuvent ne pas être présents dans les fèces du donneur, ce qui pourrait affecter l'appariement entre l'odeur de l'aliment perçue dans les fèces et l'odeur de l'aliment lui-même, empêchant par conséquent l'acquisition de la TSPA. Plusieurs études ont montré que la TSPA indirecte était possible chez la souris lorsque le support d'information était composite[9]. La diversité des marqueurs odorants caractérisant l'aliment pourrait alors jouer un rôle primordial dans l'identification de l'odeur alimentaire présente dans les fèces. Afin de tester cette hypothèse, nous avons utilisé deux aliments de composition identique qui ne diffèrent que par l'ajout d'une molécule odorante simple. Testés chez des souris femelles, nos résultats ont montré qu'une molécule odorante simple en tant que support d'information alimentaire n'était pas suffisante pour induire une TSPA indirecte. Des analyses chimiques n'ont pas révélé, pour chaque aliment testé, la présence de la molécule odorante simple dans les fèces de souris, suggérant que la dégradation de ces marqueurs odorants pendant le processus digestif a empêché l'appariement entre l'odeur alimentaire présente dans les fèces et celles présentées durant le test de choix. Ceci souligne le fait que le système digestif est une contrainte possible de la TSPA indirecte en favorisant le risque d'altération de l'information alimentaire dans les fèces. Toutefois, les travaux montrant l'acquisition de la TSPA indirecte avec l'utilisation d'odorant composite indique que cette contrainte semble supprimée lorsque les marqueurs odorants sont multiples. En utilisant un procédé qui limite la dégradation des molécules, nous avons testé la TSPA indirecte lorsque l'information caractérisant les deux aliments était représentée soit par une molécule odorante simple, soit par un bouquet de molécules odorantes. Contrairement aux résultats obtenus avec un bouquet de molécules odorantes, la TSPA indirecte n'a pas été clairement mise en évidence lorsque l'information alimentaire était représentée par une molécule odorante

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[9] Arakawa, H. et al. (2013). The receptor Guanylyl Cyclase type D (GC-D) ligand uroguanylin promotes the acquisition of food preferences in mice. *Chemical Senses, 38*, 391–397.

simple, malgré cette fois, la présence de la molécule dans les fèces, confirmée par des analyses chimiques. Ceci met en évidence que la multiplicité des marqueurs odorants caractérisant l'aliment lève non seulement la contrainte associée à la dégradation des molécules durant la digestion mais semble également être une condition nécessaire à la détection de la source alimentaire dans les fèces. Dans des conditions similaires, nous avons montré que la TSPA directe entre femelles familières était efficace lorsque le support de l'information était une molécule odorante simple. Ainsi, alors que la TSPA directe semble être limitée par des contraintes sociales, elle permet toutefois une évaluation plus précise des aliments consommés par les congénères que la voie indirecte. Nous suggérons que la perception simultanée d'informations complexes caractérisant le donneur pourrait interférer avec les informations alimentaires présentes dans les fèces. Dans ce cas, la multiplicité des marqueurs odorants pourrait alors être un élément essentiel pour permettre la détection de l'aliment consommé par le congénère.

La présence simultanée de différents types d'information dans les fèces caractérisant à la fois le donneur et son alimentation nous amène au troisième et dernier point abordé dans cette thèse. Bien que la TSPA indirecte puisse réduire les contraintes associées à la présence d'un congénère, les informations caractérisant le donneur peuvent être particulièrement utiles aux souris dans le cadre d'autres comportements sociaux tels que la territorialité et la reproduction[10]. Chez la souris domestique, les mâles sont territoriaux et les marques odorantes fournissent des informations pertinentes sur de potentiels compétiteurs ou de potentiels partenaires sexuels. Comme pour toutes les femelles de mammifères dont le cycle de reproduction demande beaucoup d'énergie, la nourriture représente, en revanche, pour les femelles de cette espèce une ressource essentielle. Nous avons alors émis l'hypothèse que, selon les différents besoins et priorités biologiques des souris mâles et femelles, les indices alimentaires présents dans les fèces pourraient être négligés ou, au contraire, privilégiés, par rapport aux autres indices caractérisant le congénère, affectant ainsi les conditions dans lesquelles cet apprentissage serait fonctionnel. Pour tester cette hypothèse, nous avons évalué l'acquisition de la TSPA indirecte, chez les mâles et les femelles, en faisant varier les caractéristiques du donneur. Nos résultats ont indiqué que les

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[10] Arakawa, H. et al. (2008). Scent marking behavior as an odorant communication in mice. *Neuroscience & Biobehavioral Reviews*, *32*, 1236–1248.

femelles utilisaient les informations relatives à un nouvel aliment provenant des fèces d'une autre femelle, qu'elle soit familière ou non, ainsi que celles provenant des fèces d'un mâle non familier. Chez les mâles, cependant, la TSPA indirecte n'a pas été clairement établie lorsque les mâles flairaient les fèces d'un autre mâle, qu'il soit familier ou non, ainsi que les fèces d'une femelle non familière. En revanche, une habituation préalable à l'odeur d'une femelle non familière, mais pas à celle d'un mâle non familier, a permis l'établissement de la TSPA indirecte chez les mâles. Cette voie indirecte a été également établie chez les mâles lorsque les fèces étaient ceux d'un mâle sexuellement immature. Enfin, nos résultats ont montré que la présence de fèces d'un mâle non familier était suffisante pour altérer l'acquisition de la TSPA lorsque l'information alimentaire provenait d'une femelle donneuse auxquelles les observateurs étaient préalablement familiarisés. Nous suggérons que ces résultats sont fortement liés à une sélection des informations lors de l'investigation des fèces d'un congénère, dépendante des stratégies de reproduction de chaque sexe. En effet, différentes pressions de sélection ont conduit les mâles et les femelles à développer des stratégies différentes. Chez la souris domestique, le succès reproducteur de la femelle est principalement déterminé par sa capacité à élever sa progéniture après la fécondation [11]. De ce fait, élargir son répertoire alimentaire représente pour elle une opportunité d'assurer ses dépenses énergétiques nécessaires à son cycle de reproduction. Les stratégies reproductives des mâles, en revanche, sont directement liées à la territorialité et à la recherche de partenaires sexuels. Ceci pourrait expliquer que les mâles accordent plus d'importance aux caractéristiques de leur donneur, clé de leur succès reproductif, qu'à l'information sur une nouvelle ressource alimentaire d'importance stratégique moindre. Ainsi, ces résultats soutiennent l'idée que dans le contexte de la TSPA indirecte, tandis que les femelles sélectionnent systématiquement les informations sur de nouveaux aliments potentiels, les mâles semblent être davantage préoccupés par les informations caractérisant les congénères. Nos résultats dévoilent ainsi la possibilité d'une différence sexuelle sous-jacente dans l'acquisition de la TSPA indirecte, qui semble être fortement dépendante des préoccupations des individus.

L'ensemble des résultats de ce projet de thèse apporte une vision plus large des conditions dans lesquelles la TSPA pourrait être utilisée chez la souris

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[11] Speakman, J. R. (2008). The physiological costs of reproduction in small mammals. *Philos Trans R Soc Lond B Biol Sci.*, *363*, 375–398.

domestique. En effet, pris tous ensemble, ces résultats révèlent l'importance du contexte social dans laquelle l'information est perçue par les souris pour déterminer leurs choix alimentaires.

Nous avons vu que l'acquisition de la TSPA directe peut être grandement affectée par les contraintes sociales de l'espèce, réduisant ainsi, chez la souris domestique, son utilisation à des congénères familiers. Toutefois, elle lève également des contraintes physiques, qui offre l'opportunité aux souris d'avoir une évaluation fine des aliments exploités par leurs congénères. Dans ce cas, la TSPA directe pourrait s'avérer utile pour diffuser plus rapidement au sein d'un groupe social des informations précises portant sur de nouvelles ressources alimentaires.

A l'inverse, la TSPA indirecte dispense d'un niveau de tolérance sociale autorisant un contact direct et permettrait ainsi aux souris d'accroître sensiblement la diversité de leurs sources d'information. Cependant, du fait des contraintes liées à la digestion de l'aliment, les informations véhiculées par cette voie de transmission ne devraient pas ou difficilement permettre aux souris une distinction entre deux aliments de composition très proche et porteraient davantage sur un type général d'aliment. De plus, bien que nous ayons démontré qu'une TSPA indirecte soit possible entre individus non familiers, cette voie présente également des contraintes sociales dues à la sélection par les individus des différents types d'informations présents dans les fèces. Ainsi, compte tenu de leurs préoccupations, les femelles semblent être les meilleurs vecteurs à la diffusion de l'information au sein de la population. Par voie indirecte, elles peuvent utiliser les informations provenant de tout type de congénères et représentent les médiateurs les mieux acceptés par l'ensemble des différents types d'individus de la population.

Par les contraintes et les affranchissements propres à chaque voie, la TSPA directe et indirecte pourraient donc être complémentaires dans des conditions naturelles, chacune étendant les conditions de diffusion d'une information portant sur une nouvelle ressource alimentaire chez les rongeurs. Des études menées en milieu naturel sur des populations sauvages pourraient permettre de transposer ces résultats à un niveau populationnel et d'évaluer en particulier l'impact d'individus possédant des informations clefs sur les stratégies alimentaires d'une micro-population. Ce travail de thèse a contribué à répondre aux questions concernant les stratégies alimentaires des souris mais en pose davantage sur les mécanismes sous-jacent de la TSPA. En effet, nos résultats comportementaux suggèrent que des processus complexes tels que les processus perceptifs, attentionnels, émotionnels et motivationnels sont impliqués dans cet apprentissage. Cette thèse ouvre des voies pour mieux comprendre le traitement et la hiérarchisation des informations olfactives chez les souris.

Sommaire - Summary

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General introduction

Foraging behavior: to eat or not to eat, that is the question

To survive in natural environments, foraging behavior is fundamental for any animal species. Because animals live in a dynamic and complex environment, selecting an adequate diet is not a simple task. Indeed, animals are conducted to make efficient food choices in order to choose food items that provide all the nutrients needed for self-maintenance and avoid eating any toxic item they may encounter.

Beyond the physiological, life-sustaining functions of eating, foraging behavior is intimately involved with other aspects of individual and social behavior. Foraging animals obtain food and information about food resources during their feeding activity. Of course, animals also acquire and use information when they choose mates, defend territories or avoid predators. However, the idea that animals may act on and seek to obtain information about food resources connects foraging models to central questions in biology. For several decades now, ethologists, biologists and psychologists try to understand how animals learn to select food products in their environment (reviewed by Rozin, 1976; Galef, 1996; Galef & Giraldeau, 2001) and avoid toxic items they might encounter when they sample unfamiliar potential foods in order to increase their food repertoire (reviewed by Garcia, Hankins, & Coil, 1977; Galef, 1996).

In a general context, foraging behavior has been the subject of extensive theoretical and empirical research (Stephens & Krebs, 1986). It is assumed that an animal that can feed more efficiently than others will benefit of its acquired resources to improve its fitness (survival and reproductive success). In order to understand the complexity and diversity of animals' foraging behavior, different foraging theories have been developed.

One of the major foraging theories used to predict the foraging behavior of animals by means of mathematical models is the *optimal foraging theory*, which was first developed by Emlen (1966) and MacArthur and Pianka (1966). According to Pyke, Pulliam, and Charnov (1977), these models used a similar approach, in that "they all assume that the fitness of a foraging animal is a function of the efficiency of foraging measured in terms of some "currency" (Schoener, 1971) -usually energy- and that natural selection has resulted in animals that forage so as to maximize this fitness". Based on this concept, extended studies have developed several complex models to predict the foraging behavior of animals (Pulliam, 1974; Charnov, 1976). Pyke et al. (1977) reviewed that during foraging, animals are conducted to evaluate the situation according to the following four categories: (a) which food types to eat (i.e., optimal diet choice); (b) which patch type to feed in (i.e., optimal patch choice); (c) optimal allocation of time to different patches; and (d) optimal patterns and speed of movements. Thereafter, a fifth category was developed: the central place foraging (Orians & Pearson, 1979). In this situation, the animal has a central foraging base, mostly its nest, from which it continues to feed and where it frequently returns with all or part of its harvest obtained during foraging.

For several years, literature on optimal foraging theory has been reviewed a number of times (Pyke, 1984). Nevertheless, optimal foraging theory has engendered considerable controversy (Pyke, 1984; Ollason, 1980). The most critical view of optimal foraging theory is that several hypotheses on which the models were based are unrealistic (Pyke, 1984). A first criticism has been to consider that animals have access to all the information that enables them to evaluate the costs and benefits associated with the different possible choices of a situation (Sih, 1992). Gray (1987) criticizes the fact that increasing foraging efficiency does not necessarily increase individual fitness. Pierce and Ollason (1987) also argue about the limitations of the theory and consider, among other things, that optimal strategies may not occur in natural conditions.

At the same time, the application of optimal foraging theory to understand animal behavior has been criticized because it focuses only on the relationship between forager and resource (Pierce & Ollason, 1987; Delton & Robertson, 2012) and in many studies the models used do not consider relationships between foragers. Thus, strategies that can be employed in a social context, such as competition, learning and, imitation, are omitted from these models. New models, called *social foraging theory*, inspired by optimal foraging theory have been developed incorporating the advantages and constraints of group formation on foraging behavior (Giraldeau & Caraco, 2000). This theory considers that social animals, because they select the resources that they need, take into account information from multiple sources, including individual experience and social information, which increases their capacity to exploit their environment and the consequent maximization of their fitness (Webster & Laland, 2012). As early as the 1970s, the research has seen a striking increase in the number of studies of the role of social interactions in shaping food selection. Thanks to the established knowledge from earlier research describing nonsocial factors that influence food selection by animals, studies of social influence on the food choices of animals have been particularly fruitful. The evidence clearly demonstrates the importance of socially acquired information in shaping the development of food selection in vertebrates.

Social influences on the food selection in vertebrates

There are different ways for an individual to obtain information about new food sources (figure 1). The first is to use *personal experience* by identifying a new type of food (feeling it, tasting it). Through a tactic of trial-error, the animal incorporates a new type of food into its food repertoire or rejects it (Danchin, Giraldeau, Valone, & Wagner, 2004). The success of omnivorous and generalist species depends on their propensity to test new food items in order to expand their diversity of food resources, while remaining cautious in order to limit the risk of ingesting poisonous substances (Freeland & Janzen, 1974; Glander, 1982). A partial solution is food neophobia, i.e. the hesitancy to eat novel foods (Barnett, 1963). However, in the long term, food neophobia could be maladaptive, because omnivorous and generalist species increase chances of survival through variety in the diet. Consequently, a balance between the need for variety and caution with regard to potentially dangerous resources should emerge. Indeed, neophobia towards new food items is a behavioral response that allow to decrease the ingestion of substances in large quantities and thus reduces the risk of poisoning (Glander, 1982; Freeland & Janzen, 1974). Nevertheless, ingestion of a small amount of food is sufficient to induce post-ingestive effects, leading the animal to avoid or accept that food in its diet repertoire. However, personal experience has disadvantages because in addition to being risky, this strategy is costly to the individual in time and energy (Dall, Giraldeau, Olsson, McNamara, & Stephens, 2005). These costs have favored the development of other complementary or alternative strategies such as the exchange of social information (Templeton & Giraldeau, 1996).

By interacting with others and observing their interaction with the environment, individuals can acquire *social information*. During their daily activities, animals can coincidentally provide information that can be used by other conspecifics. Thus, from Galef and Giraldeau (2001): social information in the foraging context “depends most often not on specialized or co-evolved signals, but on information-bearing ‘cues’ or ‘signs’ that do not appear to have been shaped by natural selection for intraspecific communication”. Social cues can be provided by the location of other individuals with similar needs, in the presence of the conspecifics (Galef & White, 1998) or by the observation of their behavior from a distance (Buckley, 1997). Social information can also involve public information (Valone, 1989), when information is extracted from conspecifics without any need of their presence (Galef & Buckley, 1996; Danchin et al., 2004). Benefits of using social information consist in reducing costs related to strategies by trial and error and to provide additional information with respect to personal information, which may allow a more accurate estimate of current environmental conditions (Doligez, Cadet, Danchin, & Boulinier, 2003). Naturally, the presence of this type of strategy will depend on the life characteristics of each species. Indeed, social influences are more widely spread among species that live in groups or regularly encounter conspecifics in their environment. Generalist species are also more likely to be exposed to a new diet and tend to rely more on social cues to define foods that are fit for consumption (Dewar, 2004).

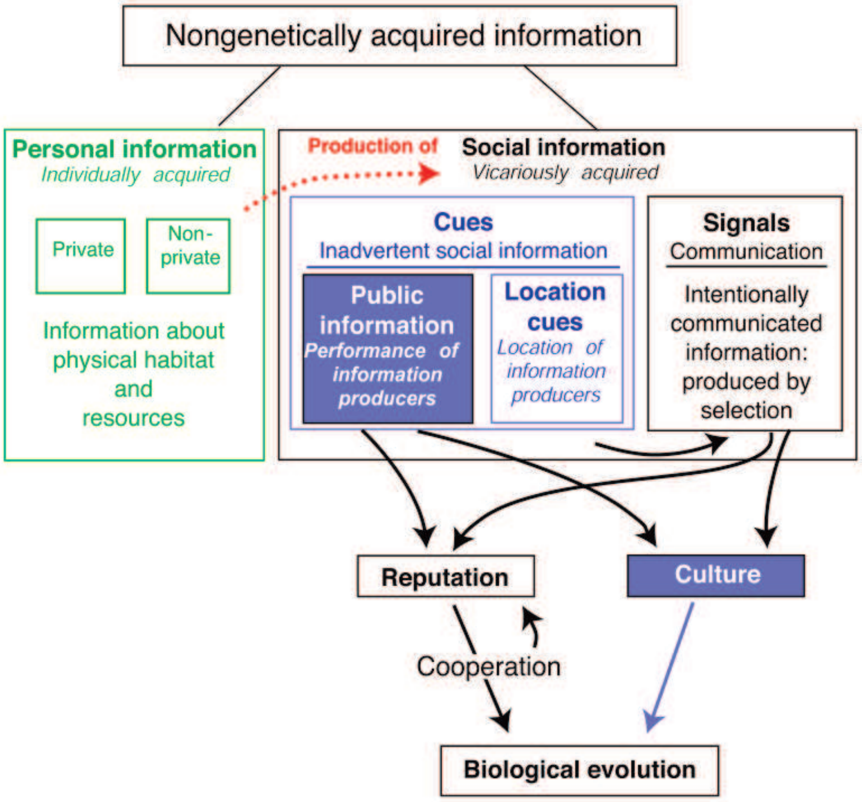

Figure 1 – Representation of the different forms of non-genetically acquired information. Personal information is acquired individually by interacting with the physical environment and by identifying a new food source. The interaction can generate both private information such as information on palatability of the food (inaccessible to others) and non-private information that produces social information such as post ingestive effects (red arrow). Social information can depend on specialized or co-evolved signals but in the foraging context, it is most often produced inadvertently as a cue. Inadvertent social information can indicate both the spatial location of resources (based on the location of the information producers) and cues produced by the performance of others, called public information. Public information may play a major role in cultural transmission and evolution (after Danchin et al., 2004).

According to Galef, the adaptive value of social influences lies in its selective use (Galef, 1995). Since the social environment differs in time and space, individuals must take into account the context in which they find themselves when acquiring social information. An individual may choose to acquire personal information by interacting with its abiotic environment or may choose to acquire social information from conspecifics. Different strategies for using social influences have thus been theorized and can be grouped around two questions: "when" and "from whom" to extract social information (Laland, 2004). Individuals are not necessarily aware of the use of these strategies, as opposed to the term employee referring to a high cognitive process (Heyes, 2012). They can follow a general rule inherited genetically or learned during their lifetime (Laland, 2004).

Across the lifespan, individuals evolve in different social and environmental contexts that will enable them to acquire information about the environment that surrounds them and especially about food resources. Studies on social influences in the foraging context were focused on these different periods when the social context varies considerably.

Prenatal influences

Even before birth, the ability of mammals to perceive flavors begins *in utero* with the development and early functioning of the gustatory and olfactory systems. Indeed, some chemical compounds cross the placental barrier and can reach the fetus (Leon et al., 1987; Hepper, 1988; Pacifici & Nottoli, 1995; Myren, Mose, Mathiesen, & Knudsen, 2007). Because amniotic fluid contains molecules derived from the mother's diet, learning about food flavors begins in the womb. Thus, Smotherman (1982) found that adult rats (*Rattus norvegicus*), whose mothers have been given an injection of apple juice into their amniotic fluid during gestation, showed a greater preference for apple juice during a choice between apple juice and water, than rats whose mothers had received injections with water while gestation. However, the flavor cues do not need to be injected in order to have their effect: young rats whose mothers have been fed garlic during gestation showed, after weaning, a preference for the odor of garlic (over onion) (Hepper, 1988). Similarly, studies in human suggests that flavors, when presented repeatedly within the amniotic fluid, influence the food preferences of infants and this immediately after birth (Mennella, Jagnow, & Beauchamp, 2001; Faas, Spontón, Moya, & Molina, 2000). For example, infants whose mothers consumed anise flavor during pregnancy showed a stable preference for anise odor and fewer negative facial responses in response to a anise flavor compared to infants whose mother had not consumed any food with anise flavor during pregnancy (figure 2) (Schaal, Marlier, & Soussignan, 2000). This phenomenon has been observed in the rat and humans as well as in other mammals such as the rabbit (*Oryctolagus cuniculus*) (Bilkó, Altbäcker, & Hudson, 1994; Coureaud, Schaal, Hudson, Orgeur, & Coudert, 2002; Semke, Distel, & Hudson, 1995), the domestic pig (*Sus domesticus*) (Langendijk, Bolhuis, & Laurenssen, 2007; Figueroa, Solà-Oriol, Vinokurovas, Manteca, & Pérez, 2013) and the dog (*Canis familiaris*) (Hepper & Wells, 2006). As well as prenatal influences can shape food preferences of young pups, they can also lead to food aversion. When pregnant rats were subjected to garlic essential oil and 45 min later to lithium chloride (a substance which induce a sickness onset which is rapid but not long lasting), this induced a strong aversion to garlic in the progeny, which lasted until after weaning (Gruest, Richer, & Hars, 2004).

In conclusion, prenatal influences can be considered as initial experience for individuals which serves as a basis for the continuous development of food preferences throughout life and which is shaped by the interplay of biological, environmental and social factors.

Influences during nursing

We have seen that during gestation, the mother is a social individual who can influence the food choices of its pups, but she can also play a predominant role during nursing. Several studies demonstrate that flavors of foods that a female rat (or human) eats while lactating can alter the flavor of her milk (Galef & Henderson, 1972; Capretta & Rawls, 1974), and second, that exposure to food flavors in mother's milk affects the food preferences of pups at weaning (Galef & Sherry, 1973; Galef & Henderson, 1972; Bronstein & Crockett, 1976; Schaal et al., 2000; Mennella et al., 2001). For example, rats' pups, when they

(a) Responses by newborns of anise-consuming mothers

(b) Responses by newborns of non-anise-consuming mothers

Figure 2 – Representative examples of facial expressions of awake newborns exposed to anise odor stimuli. (a) Positive facial configurations by newborns of anise-consuming mothers (b) Negative facial configurations by newborns of non-anise-consuming mothers (modified after Schaal et al., 2000).

were breastfed for a few hours by a female having consumed a distinctively flavored food, showed, after weaning, an enhanced preference for a similar diet. However, rats' pups showed no similar preference after a female who had eaten the same flavored food, provided them with maternal care but did not breastfeed them (Galef & Henderson, 1972). The acquisition of food aversion can also pass through milk consumption. Rat pups that had been made ill immediately after they were fed milk from a lactating rat eating a distinctively flavored diet exhibited, at weaning, an aversion for diets which have a similar odor (Galef & Sherry, 1973). In rabbit, it has been shown that the pups respond immediately to birth with a predisposed signal, a short carbon chain molecule contained in the milk effluent of any female rabbit, 2-methyl-2-butenal (Coureaud, Schaal, Langlois, & Perrier, 2001; Schaal et al., 2000; Coureaud et al., 2010). The presence of this compound in the mother's milk plays a predominant role in the appetitive learning of odorant compounds and in particular of food odors (Coureaud et al., 2002).

Influences during weaning

One of the critical moments for the development of food selection is the weaning period. Although adopting the behavior of others may not always be an advantageous choice for an individual, the benefits of social influences, particularly to naive young animals, should most often outweigh any potential costs. Indeed, to survive, a young animal has to learn rapidly to select a nutritionally balanced diet before it exhausts its internal reserves and without endangering itself by ingesting toxic items. Thus, a naive young animal, whenever possible, would benefit from the interactions it has with the adult conspecifics of its species. Again, the mother will play an essential role in acquiring food information during weaning but the adults of the group could also influence the choices of the young. Indeed, adults are individuals that have acquired patterns of behavior allowing them to avoid the ingestion of toxins and to select an adequate diet. In social species, the adults of the group are often present when the young have to acquire their independence. Consequently, naive juveniles can use the behavior of adults to guide development of their own behavioral repertoires and the acquisition of social information could help to decrease the costs associated with individual trial-and-error learning.

The role of maternal interaction on the development of food preferences in young animals during the weaning period has been described in a multitude of studies (reviewed by Galef, 1996). In this manuscript, I will refrain from giving a thorough review of all the studies dealing with this subject and I will only present some general results. By rewarding electrical stimulation of the brain, Wyrwicka (1978) induced in mothers cat (*Felis catus*) the consumption of unusual food such as banana. After repeated interaction with their mother cat while she was eating the unusual food, kittens are disposed to eat from exactly the same site as their mother. This consumption was facilitated even many weeks later. Sheep (*Ovis aries*) can also induce their young to begin feeding on unfamiliar foods (Key & Maciver, 1980; Thorhallsdottir, Provenza, & Balph, 1990). When lambs received wheat for the first time during weaning, they consumed more this novel food in the presence of their mother who was trained to eat wheat than when they were left alone (Lynch, Keogh, Elwin, Green, & Mottershead, 1983). Influences of maternal interaction on food choices and/or feeding sites have been also observed in other vertebrate's species such as chicks (*Gallus gallus*) (Stokes, 1971), young Belding's ground squirrels (*Spermophilus beldingi*) (Peacock & Jenkins, 1988), young meerkats (*Suricata suricatta*) (Ewer, 1963), pups spiny mice (*Acomys cahirinus*) (McFadyen-Ketchum & Porter, 1989) and infant chimpanzees (*Pan troglodytes*) (Silk, 1978).

However, as stated above, the adults of the group could also influence the choices of the young. In several species, when young animals start feeding on solid foods, they are more attractive to feeding sites and food items where there is the presence of adults. For example, in meerkats, pups are neophobic towards unfamiliar foods but will incorporate them into their diet repertoire after interacting with adult group members. In the absence of adults, pups refused to eat hard-boiled egg, but when they were exposed to an adult of their group who ate this food, pups rapidly learned to eat egg. Similarly, when pups see an adult consuming scorpions, they are less reticent to sample the prey and subsequently incorporate it into their diet repertoire (Thornton, 2008) (figure 3). In rat, Galef and Clark (1971) observed that wild rat pups eat for the first

Figure 3 – Adult and young meerkats (*Suricata suricatta*) consuming together a scorpion prey. ©David Macdonald / www.arkive.org

time under exactly the same circumstances: each ate while an adult was eating, and each ate at the site where the adult was eating, not at a nearby feeding site where no adult was feeding.

In rat, it would also appear that the only presence of an adult (anesthetized rat) or olfactory cues provided by adults at feeding sites is sufficient to induce a preference for a marked food site (Galef & Heiber, 1976; Galef, 1981; Laland & Plotkin, 1990, 1993; Galef & Clark, 1971). While eating, adult rats deposit residual olfactory cues near the food source. These olfactory cues are attractive to rat pups, who feed more on sites marked by conspecifics than on unmarked ones (Galef & Heiber, 1976; Laland & Plotkin, 1990, 1993). Although being attracted to a site does not necessarily mean that young people will select the same food as adults, it does increase the likelihood of consuming similar foods.

Finally, some studies have focused on the social influence of food avoidance during weaning. Results shown that young do not seem to learn directly to avoid foods that adults in their group or mother avoid (Galef, 2012). On the contrary, it appears that they learn to eat the food consumed by adults and because they prefer to consume familiar foods, they avoid foods that adults do not consume (Galef & Clark, 1971; Galef, 1985; Mirza & Provenza, 1994).

Influences in adulthood

Even in adulthood, social influences may continue to play an important role in food selection, especially when individuals need to expand their food repertoire. In many species, the presence of conspecifics at a feeding site attracts conspecifics to that site and causes them to begin eating there. In adult hens, after the observation of a demonstrator pretrained to peck one of two differently colored keys to obtain access to a food hopper, observers spent more time facing the keys, performed more key pecks and showed a significant bias toward pecking the same color key as that pecked by their respective demonstrators (Nicol & Pope, 1992; Nicol, 2004). Similarly, male red-wing blackbirds (*Agelaius phoeniceus*) that observe conspecifics eating from yellow or green cups subsequently prefer to eat from similar cups, whereas blackbirds that had watched conspecifics eating from the same cups and then becoming ill after feeding avoided to eat in similar cups (Mason, Dolbeer, Arzt, Reidinger, & Woronecki, 1984). The use of visual cues to select foods to consume or avoid has also been observed in some primate species (Jouventin, Pasteur, & Cambefort, 1977). Visalberghi and Fragaszy (1995) showed that capuchins (*Cebus apella*) ate significantly more of novel foods when in the presence of group members eating the same novel foods, whereas with familiar foods the increase was not significant.

However, vision is not the only modality that can be used by animals to imitate the feeding behavior of others. In the mandrills (*Mandrillus sphinx*) and olive baboons (*Papio anubis*), when an individual eats, a conspecific may smell the masticated food, which allows it to know new edible foods without risking to taste them (Laidre, 2009). Domestic dogs are also able to learn to prefer foods that conspecifics have eaten (Lupfer-Johnson & Ross, 2007). In this experiment, Lupfer-Johnson and Ross fed dogs with food flavored with either basil or thyme. After interaction with one of this dogs, naive dogs are disposed to eat the similar flavored diet in a choice test. The interactions that occur between the two dogs suggest that this social influence occurs by means of olfactory cues. Similarly, after a social interaction with a familiar demonstrator, male and female observer pig preferred flavors previously eaten by the demonstrator over another flavored diet (Laidre, 2009; Figueroa, Solà-Oriol, Manteca, & Pérez, 2013).

A number of studies highlighted species able of learning from conspecifics about new food resource. But finally, social influences are perhaps best understood in rodents and especially, in Norway rats, thanks largely to the work of Galef and his coworkers (reviewed by Galef, 2012).

Social transmission of food preference (STFP) in rodents

Box 1. Use of the term *Social transmission of food preference*

Social transmission...

The term *social transmission of food preference* was described for the first time by Galef as a form of social learning: a behavior socially transmitted, in that "social interaction increases the probability that one individual will come to independently exhibit a behavior initially in the repertoire of another" (Galef, 1976). In this case the term *social learning* is used in its broadest definition: it is theoretically neutral and suggests a dichotomy between learning that is influenced by observation of, or interaction with, another animal (typically a conspecific) or its products (Hoppitt & Laland, 2013) and instances of *asocial learning* in which behavior acquisition is not influenced by interaction with others (Heyes, 1994; Galef, 1976). To begin with, any form of social learning requires an observer and a demonstrator (or donor), who performs the behavior later reproduced in whole or part by the observer. To qualify as learning rather than socially elicited or facilitated behavior, the observer's performance must take place at a later time, away from direct influence of the demonstrator (Shettleworth, 2010).

...of food preference

The notion of *food preference* used by Galef is debatable. Indeed, the term *preference* refers to the selection of one item over others (Birch, 1999). However, this social behavior does not induce a strict selection of one food among others but facilitates its consumption by the socially informed individual compared to that of a naive individual. The use, in laboratory conditions, of a choice test between two new food items facilitates the demonstration of this phenomenon but somewhat revives this ambiguity. Indeed, choice tests are generally used to determine the preferences of an individual between two or more items (Bateson, 2004). However, the acquisition of the social transmission of food preference was assessed, not by comparing the observer's consumption between the two diets, but by measuring the proportion consumed for one of the two diets and comparing it with a control group. In this case, even if there is a preference bias between the two diets presenting during the choice test (for example, a diet that is more palatable than the other), only the increase in consumption for the demonstrator's food will change the value of the proportion measured.

Direct STFP: Social transmission of food preference through interaction with a conspecific

In 1983, two research teams highlighted in laboratory conditions that during an encounter between a recently-fed rat (referred to as "demonstrator" hereafter) and a naive conspecific (referred to as "observer" hereafter), information present in the breath of the demonstrator pass to observer increasing the observer's subsequent consumption for the food its demonstrator ate (Galef & Wigmore, 1983; Posadas-Andrews & Roper, 1983) (figure 4).

This social influence, called *social transmission of food preference (STFP)* (Box 1) was observed in several additional species of rodents such as mice (Valsecchi & Galef, 1989; McFadyen-Ketchum & Porter, 1989), gerbils (Valsecchi, Choleris, Moles, Guo, & Mainardi, 1996) and hamsters (Lupfer, Frieman, & Coonfield, 2003).

Social interaction: key element of the STFP? Detailed analysis indicates that the socially-transmitted preference is not due to simple exposure to the flavor of food clinging to the fur of the demonstrator rat (Galef, 1991). By comparing (a) the food consumption of rats that interacted with demonstrators, with (b) rats that were simply exposed to flavored food during the social phase, Galef and his associates showed that a simple interaction with a demonstrator during thirty minutes was sufficient to induce a durable STFP. On the other hand, simple exposure to flavored food did not induce any preference in their test, whether the food choice was made 15 min or 24 hr after the social phase. Thus, Galef and his team highlighted that elements from a conspecific are essential for the establishment of an STFP (Galef & Wigmore, 1983).

However, the interaction itself with the conspecific could provide a particular context that could facilitate the consumption of the diet consumed by the demonstrator. Thus, researchers questioned whether the interaction between individuals was crucial or whether the presence of the conspecific alone was sufficient to induce an STFP. To answer this question, a series of experiments was carried out by varying the demonstrator model presented during the social phase (awakened demonstrator, anesthetic demonstrator, artificial demonstra-

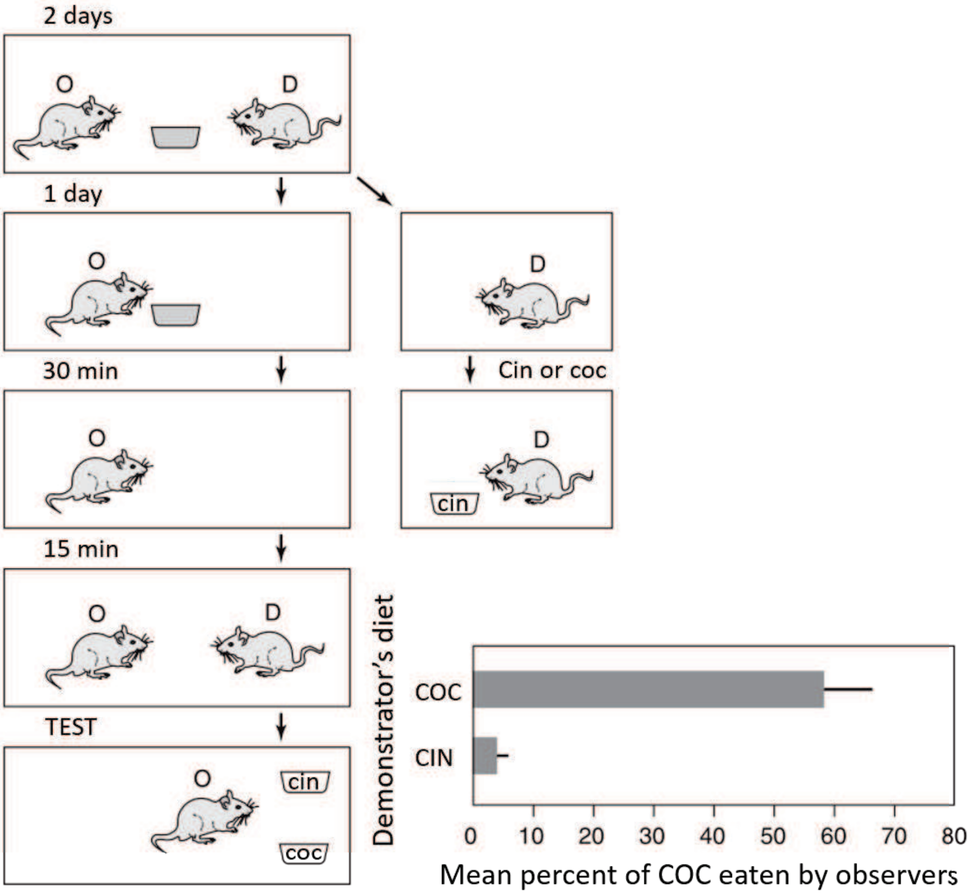

Figure 4 – Design and results experiments establishing the direct social transmission of food preference in Norway rats (*Rattus norvegicus*) in the study of Galef and Wigmore (1983). D: demonstrator; O: observer; COC: cocoa-flavored food; CIN: cinnamon-flavored food. Data corresponds to the mean percent of COC consumed in the first 12 hours of the test in the two experimental groups whose demonstrators consumed CIN or COC diet (modified after Shettleworth, 2010).

tor). For each experiment, the demonstrators carried on their information about a flavored food. The results revealed that the presence of an anesthetized or not conspecific was sufficient to induce STFP while the presence of an artificial demonstrator failed (Galef, Kennett, & Stein, 1985). This result suggested that the simultaneous presence of a conspecific and the food odor was necessary to induce the STFP but that the behaviors realized by the demonstrators during the interaction were not decisive in this acquisition. Failure with an artificial conspecific suggested that olfactory cues provided by the conspecific could be necessary for the establishment of the STFP.

Duration and frequency of interaction The question was also whether the duration of the interaction and the number of interactions could affect the longevity of the food preference induced in the observer. It would seem that the duration of the interaction is not a determining factor for the induction of a food preference. Indeed, even with a very short interaction time of the order of two minutes, the rat observers showed a preference for the food previously consumed by the demonstrator (Galef et al., 1985). However, to ensure the persistence of this food preference for several days, the duration of interaction is a preponderant factor and the results show that an optimal duration is between 15 and 30 min.

A second factor, relevant for the persistence of the food preference, is the number of interactions: whatever the sex of the individuals tested, the greater the frequency of interaction between the observer and the demonstrator is, the more durable the food preference is induced. A single interaction, even if repeated several days in a row, has much less effect on maintaining preference over time than several daily interactions (Strupp & Levitsky, 1984; Galef & Whiskin, 1998a). In the search for experimental conditions that would influence the longevity of food preference, Galef and his colleagues tested two parameters in female rats: 1) several interactions with the same demonstrator, or 2) a single interaction with several demonstrators. Against all odds, what most affects the longevity of preference is the number of interactions with the same conspecific and not the number of demonstrators (Galef & Whiskin, 1998a). Similar results were obtained in female mice and showed that having one or four demonstrators carrying the same diet information did not produce a statistically different preference for that diet (Choleris, Guo, Liu, Mainardi, & Valsecchi, 1997).

Characteristics of the demonstrator This type of social influence takes place within the complex framework of interactions that may be affected by such factors as dominance hierarchies, familiarity's degree, age and sex of interacting individuals. Thus, a third point that has been studied is the demonstrator's characteristics.

In female laboratory rats, after the simultaneous presentation of a familiar demonstrator and another one unfamiliar, the observer tends to prefer the food ingested by the unfamiliar demonstrator (Galef & Whiskin, 2008). The authors explained this result by an olfactory exploration behavior called "recognition sniffing", an identification practice found in a wide variety of species, and which is more intensive and prolonged when individuals interact with unfamiliar conspecifics (Barnett, 1963).

The age of the demonstrator could also have an influence. As we have seen previously, young individuals mainly use adults to obtain information on the food to be consumed. Indeed, by survival to adulthood, adult rats demonstrate the adequacy of their food repertoire. However, young individuals, because of their inexperience, may feed on poor quality food and do not provide a fully reliable social context in which individuals transmit information. Despite theoretical justification, studies in the rat failed to provide evidence of an effect of age of demonstrator rats in the acquisition of the STFP (Galef, Kennett, & Wigmore, 1984). The age of demonstrator rats did not affect either the longevity of food preferences induced in adult female observer rats (Galef & Whiskin, 1998a). However, results of an experiment in female mice indicated that the STFP was in part an age-dependent phenomenon (Choleris et al., 1997). In this study, the authors showed that the longevity of food preferences induced in adult female observer mice was reduced when the demonstrator was a juvenile.

Finally, it is assumed that social learning can be influenced by important sexually dimorphic social constraints as well as by attention, motivation and perceptual mechanisms, which have important differences between females and males (Sanchez-Andrade, James, & Kendrick, 2005; Daniel, 2006). Among the several neurobiological systems involved in the regulation of social behavior, neurohormonal mechanisms seem to play a predominant role. In particular, the neuropeptides oxytocin, arginine–vasopressin and estrogens have been shown to play a facilitatory role during the acquisition of the STFP, explaining in part the sex differences in social information processing (Choleris, Clipperton-Allen, Phan, & Kavaliers, 2009; Sanchez-Andrade et al., 2005; Clipperton, Spinato, Chernets, Pfaff, & Choleris, 2008; Choleris et al., 2013; Choleris, Clipperton-Allen, Gray, Diaz-Gonzalez, & Welsman, 2011). However, although gender differences have been demonstrated in a wide range of cognitive and behavioral processes, research on these male-female differences in the STFP remains little studied. Indeed, in almost all of these studies, pairs of demonstrator and observer were generally of same sex. In the case where STFP was observed in both male-male and female-female pairs within the same experiment, a potential effect of sex was not investigated (Choleris, 1999; Choleris et al., 2009). Choleris (1999) reviewed some studies on STFP which suggest that both male and female mice and gerbils can learn from other conspecifics of same sex, with no apparent differences in acquisition between the sexes. However, they also stressed the fact that when a constraint appears during the acquisition of the STFP, sex differences in response to manipulations reinstating learning become evident. They also suggest that the observation of STFP in laboratory provide optimal conditions which could mask "underlying sex differences that can emerge during the suboptimal conditions that are more likely present in nature" (Choleris, 1999).

Robustness and limits of the STFP on food choices Effect of the STFP on food choice is so robust as a single brief interaction between a female observer rat that had learned an aversion to a palatable food source and a female demonstrator rat that had consumed that food item, resulting in half the observers abandoning their aversions and consuming the food of their demonstrator (Galef, 1986).

On the other hand, in human as in other animal species, Rozin and Zellner (1985) suggest that two main elements affect our food choices: the hedonic response when we experienced a food source (which will depend on the characteristics of the food consumed) and the social transmission of information about new food sources. As a result, the presence of contradictory asocial and social cues about a food source could affect the food choices of individuals. To evaluate the robustness of the STFP, studies consisted in habituating (with difficulty) a female rat demonstrator to consume food flavored with Cayenne pepper was performed. When exposed to Cayenne pepper, naive female rats consumed in very small quantities and show a real avoidance for such a mixture. Following the STFP procedure, observers prefer to consume this food item, even if they had the choice with another new food item that is more palatable, such as chocolate (Galef, 1989). However, as the amount of cayenne-flavored diet was increased, the effects of demonstrator female rats on their observers' intake of the cayenne-flavored diet diminished (Galef & Whiskin, 1998b).

Another limit on social influence on food choices which was observed is that the feeding preference of the observing female rats is maintained only when the information provided by the female demonstrator relates to a new food. In fact, if this food is familiar, the duration of the preference acquisition process will be brief and will depend mainly on the quality of the food to persist over time (Galef & Whiskin, 2000). Rodents therefore use the STFP as a source of information when they need to select new food and incorporate it into their food repertoire.

Indirect STFP: Social transmission of food preference via olfactory marks

Olfactory marks left by rodents constitute relevant sources of information (Laland & Plotkin, 1991), as body odors, urine and feces convey numerous olfactory cues about traits (e.g. identity, sex, and species) and states (i.e. diet, age, health condition) of individuals (Galef & Whiskin, 2000; Colombelli-Négrel & Gouat, 2006; Ferkin, Sorokin, Johnston, & Lee, 1997; Hurst et al., 2001; Osada et al., 2003).

Several studies suggest that cues deposited by conspecifics may play a role in different behavior of rodents including their feeding behavior. For example, rodents exhibit a preference for food sources that are in close proximity to social odors of conspecifics such as those found in soiled nest materials (Galef, 2012). In the rat, a food item or a food site marked by the excretory products of conspecifics are considered more attractive than those unmarked (Galef & Heiber, 1976; Laland & Plotkin, 1991, 1993). This suggests that such social cues could be beneficial for the survival of individuals and these marks could provide more information than the location of a food resource. This could in particular inform individuals about the nature and quality of foods even after conspecifics have left the area and would thus offer a useful parallel to the information transmitted via direct social interactions.

More recently, it has been shown in male mice that STFP can also be promoted by using feces of a donor conspecific (referred to as 'indirect STFP' hereafter) (Arakawa, Kelliher, Zufall, & Munger, 2013) (figure 5). The underlying mechanisms of this indirect STFP are well detailed in the literature. However, factors that influence the acquisition of this social influence have never been studied so far.

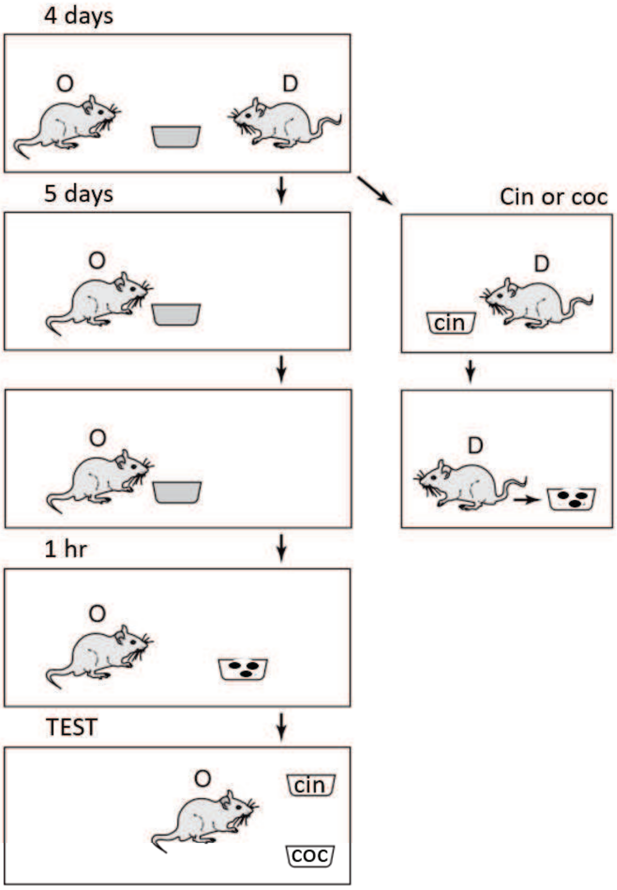

Figure 5 – Design establishing the indirect social transmission of food preference in C57BL/6J mice in the study of Arakawa et al. (2013). D: donor; O: observer; COC: cocoa-flavored food; CIN: cinnamon-flavored food (adapted after Shettleworth, 2010).

Mechanisms for acquiring the social transmission of food preference

Rodents are macrosmatic mammals that primarily use their sense of smell to evolve in their ecosystems. Concerning these species, the odors captured in the environment greatly help to the representation of environment components. The proportion of the volume of the olfactory bulb to that of the brain reflects the functional importance of the olfactory sense in rodents, particularly in comparison with that of humans. Thus, odors play a decisive role in the vital and social behaviors of rodents including the foraging behavior (Doty, 1986).

The involvement of the main olfactory system in the establishment of the social transmission of food preference (STFP) has been demonstrated and related in particular to the perception of social and food odors necessary for this learning (Sanchez-Andrade & Kendrick, 2009; Galef, 2012).

Direct and indirect STFP: a common neurobiological mechanism

The first step in understanding the acquisition of the direct STFP was to determine the nature of the information provided by the demonstrator and the type of elements that can influence the change in the feeding behavior of the observer. Because exposure to a food odor alone or carried by an artificial conspecific was insufficient to induce a food preference (Galef & Wigmore, 1983; Galef et al., 1985), it would appear that some constituents present in the breath and in olfactory marks of the demonstrator are relevant in the change of the feeding behavior of the observer. Thus, the STFP requires a specific olfactory treatment because it uses a combination of social and food odors (Galef et al., 1985; Galef & Kennett, 1987). It has been demonstrated in rats and mice that the breath blown by the snout of the demonstrator bears volatile elements which have a semio-chemical power allowing to influence the food behavior of the observer after interaction. These chemical compounds based on sulfur, carbonyl sulfide and carbon disulfide (CS_2) are essential elements to the implementation of this phenomenon, because during the interaction phase the presence of an artificial demonstrator imbibed with carbon disulfide and flavored food is sufficient to produce a dietary preference similar to that induced by the presence of a demonstrating rat (Galef et al., 1985; Galef & Kennett, 1987; Galef, 1988).

Following this discovery, the researchers then wondered how the mixture was represented at the cognitive level. Current researches in mammals suggest that the specific characteristics of odor molecules are recognized by a large family of receptor proteins (Buck & Axel, 1991). The olfactory system is composed of several subsystems, each of which can be distinguished by subpopulations of sensory neurons that express unique supplements of chemosensory receptors. These subsystems have distinct neuronal connections in the anterior brain and can respond to a set of various stimuli. The specialization of one of these subsystems in the acquisition of STFP has been demonstrated in mice. This subsystem (the GC-D/necklace subsystem) consists of olfactory sensory neurons expressing the guanylyl cyclase D-type receptor, a cytoskeletal CNGA3-sensitive channel and carbonic anhydrase CAII (Arakawa et al., 2013; Munger et al., 2010). The perturbation of the sensory transduction cascade expressing the guanylyl cyclase receptor, such as the suppression of the gene encoding this receptor, disrupts the olfactory responses to carbon disulfide and prevents the acquisition of the STFP in mice (Munger et al., 2010). This subsystem is therefore involved in the olfactory treatment of the semio-chemical molecules resulting from the breath of the demonstrator.

In a second step, research has focused on other social indicators present elsewhere than in the breath and which could induce the STFP. It has been demonstrated that the sensory neurons which express the guanylyl cyclase receptor respond to carbon disulfide but also to a natriuretic peptide: the uroguanylyl. This peptide is excreted in the urine and feces of rodents. By this discovery, Arakawa et al. (2013) showed that uroguanylyl can act as a social stimulus and promote the acquisition of the STFP via feces.

The activation of these neurons by different compounds (carbon disulfide or uroguanylyl) induces a common behavioral result and suggests that this olfactory subsystem would be specialized in the acquisition of the STFP (Leinders-Zufall et al., 2007; Munger et al., 2010).

Processing of olfactory information

In most vertebrates, the olfactory system comprises two subsystems: the main olfactory system and the accessory olfactory system. The functioning of the main olfactory system can be distinguished by two levels of organization. The first is at the periphery of the olfactory system: it concerns the arrival of the odorant molecule (box 2) in the vicinity of the olfactory mucosa and of the molecular receptors, and then the production of the signal by the olfactory neurons. The second level involves the olfactory bulb and the upper centers involved in signal processing leading to the perception and recognition of odors.

Box 2. Notion of odors and odorant molecules

The *odor* corresponds to the perception and is the result of the stimulation of the olfactory system by volatile substances, called *odorant molecules*, emanating from our environment. Odorant molecules are generally small organic molecules most of which have molar masses between 120 and 220 Da. They are variously functionalized (e.g. esters, alcohols, aldehydes and ketones), some of them carrying several functional groups. They must also be both water-soluble to dissolve in the olfactory mucosa and reach the olfactory system and fat-soluble receptors to interact with the receptors localized in the membrane of olfactory neurons. The environment is particularly rich in volatile chemical compounds emitted from a large variety of sources (e.g. plants, food, conspecifics). Most odors result from the perception of more or less complex mixtures of odorant molecules that are responsible for the activation of several olfactory receptors in the olfactory system (reviewed by Gottfried, 2006).

First level of organization: molecular reception and signal production

In vertebrates, the olfactory signal is initiated when the odorant molecules come into contact with the olfactory mucosa located on the upper part of the nasal cavities (figure 6). They activate neuroreceptor cells, more generally called *olfactory sensory neurons* (Schwob, 2002) which constitute the most represented cell category in the olfactory epithelium (about 80% of the cells).

The olfactory sensory neurons are bipolar neurons formed by an axon which projects directly to the olfactory bulb and a single dendrite that reaches up to the surface of the tissue and ends in the mucus by a protuberance swelling

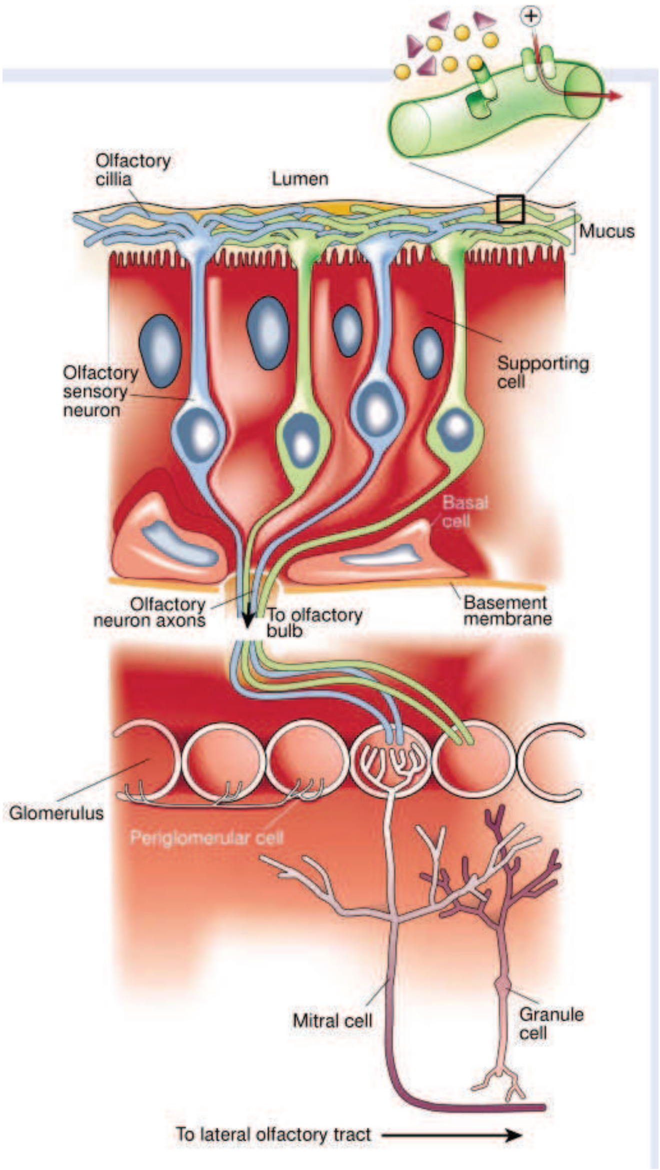

Figure 6 – Structure of the olfactory system in vertebrates. The olfactory neuroepithelium is composed of three cell types: olfactory sensory neurons, supporting cells and basal cells. Each olfactory sensory neuron expresses the same olfactory sensory receptor and the axons from all cells expressing that particular receptor converge onto one or two glomeruli in the olfactory bulb. The mitral axons leaving the olfactory bulb project widely to higher brain structures. The axons of mitral and tufted cells form the lateral olfactory tract, the only way out of the olfactory bulb to the olfactory cortex. (after Firestein, 2001).

from which project some 20–30 very fine cilia. These olfactory cilia bathe in the mucus and increase the surface area of the dendritic extremity by a factor of 30, thus promoting the interaction between the odorant molecule and the olfactory neuron. They confer on the olfactory neurons the property of being the only nerve cells directly in contact with the external environment (Graziadei & Monti Graziadei, 1978). The ciliated extremities of the neuroreceptors are the site of sensory transduction. They are lined with transmembrane receptors, called *olfactory sensory receptors*, on which the odorant molecules can bind (Imai & Sakano, 2008; Buck & Axel, 1991). In mammals, the interaction of an olfactory receptor with an odorant molecule initiates the cellular response by activation of G proteins (transmembrane proteins possessing a reception site with which the odorant molecule can bind) (Firestein, 2001) which allow the transduction of the olfactory message into nerve impulses. The axons of olfactory neurons pass through the sieve plate of the ethmoid (a perforated part of the cranial chamber) and project to the olfactory bulb at the level of the glomerular layer.

The understanding of the functional organization of the olfactory system was made possible by the work of Buck and Axel (1991) who discovered the family of genes coding for olfactory sensory receptors. In humans, there are about 250 different receptors, while rodents express more than 1000 (Imai & Sakano, 2008). Each neuron expresses only one molecular receptor, but each receptor protein can bind together all the odorants having in common a particular molecular trait recognized by this receptor (Chess, Simon, Cedar, & Axel, 1994; Malnic, Hirono, Sato, & Buck, 1999; Serizawa et al., 2000). The characteristics of the receptor fields vary according to the olfactory receptors (Malnic et al., 1999). Indeed, some receptors are selective and others are more generalist (Araneda, Peterlin, Zhang, Chesler, & Firestein, 2004; Keller & Vosshall, 2007). Conversely, depending on their functional groups, odorant molecules may be able to activate several different receptors and thus several olfactory neurons. The response profile of the sensory neurons to an odorant will depend on the affinity of the odor molecule for the olfactory receptor. Thus, depending on its chemical composition, each odorant activates a given combination of olfactory receptors and thus a specific population of sensory neurons. This accounts for a combinatorial effect at the peripheral level which is a first level of odor coding (Malnic et al., 1999).

Thus, an odorant will activate a unique set of receptors that characterize it, but sets of receptors activated by two different odorants may overlap. Consequently, odorant molecules with similar structures may be perceived differently (Laing, Legha, Jinks, & Hutchinson, 2003) and odorant molecules apparently different but having common structural characteristics can lead to similar perceptions (Sanz et al., 2008). In addition to this, when the concentration of an odorant increases, the set of activated olfactory receptors widens, which leads to a different perception of the odorant molecules depending on their concentration (Rubin & Katz, 1999).

Second level of organization: signal processing and perception of odors by olfactory nerve pathways

Principal olfactory bulb Compared to other sensory systems, the main olfactory system is a direct system of information transmission because it projects directly from the periphery to a cortical structure, the principal olfactory bulb. The olfactory bulb not only acts as a relay but is a key structure for coding, discriminating and storing odors. In mammals, particularly in rodents, it forms the most rostral extremity of the central nervous system. It is a spheroidal paleocortex which has a laminar structure in which several layers of cells and fibers are organized concentrically. These different layers participate in the reception, processing and relaying of olfactory messages. The olfactory message is encoded within the olfactory bulb in order to give a specific space-time representation of the perceived odor (Martin et al., 2012; Leon & Johnson, 2003; Gobbo, Petit, Gurden, & Dhenain, 2012; Osmanski et al., 2014).

Spatial representation of olfactory responses After having received signals from the olfactory receptors that have been activated by odorant molecules, olfactory neurons that express the same receptor converge upon one or two glomeruli (Wilson & Mainen, 2006; Firestein, 2001). Thus, each glomerulus selectively processes information from a given type of molecular receptor to odorants (Klenoff & Greer, 1998). This particular mode of connectivity allows an odorant molecule comprising several different molecular groups to activate a given set of glomeruli, thus imposing a spatial combination of activation of the bulbar glomeruli specific to the odorant molecule (Mombaerts et al., 1996; Willhite et al., 2006). This spatial combination is specific to the nature of the odorant, but also its intensity: the higher the concentration of the odorant molecule is and the higher the number of activated sensory neurons and activated glomeruli are (Rubin & Katz, 1999). The axon of the olfactory neuron that reaches a given glomerulus does not previously produce either collateral or synaptic relays. The first consequence of these anatomical data is that the information provided by an olfactory neuron has not undergone any modification (Klenoff & Greer, 1998; Mombaerts et al., 1996). If the number of olfactory neurons was compared with the number of glomeruli, it is found, in rodents, that there is a ratio of 5000 olfactory neurons per glomerulus. This ratio which varies according to species but numerical convergence is always retained. In the glomerulus, the axons of olfactory neurons form synapses with the dendrites of output neurons, called mitral and tufted cells in mammals. Most of these individual cells receive a direct excitatory input from a single type of olfactory neuron, expressing one type of odor receptor. The organization of the input olfactory neurons into the glomerulus has therefore a key feature: convergence. The existence of a territorial organization of the epithelio-bulbar projections and of a numerical convergence of the olfactory nerve fibers on the bulbar glomeruli is favorable for a signal amplification.

In the olfactory bulb, the activities of mitral and tufted cells are also regulated by an interneuron circuit (juxtaglomerular cells and granular cells) that allows communication within and between glomeruli (Cleland & Sethupathy, 2006; Shepherd, Chen, Willhite, Migliore, & Greer, 2007). The juxtaglomerular cells receive direct excitatory input from the axons of the olfactory neurons and form inhibitory synapses on the axons of the olfactory neurons in the same glomerulus. They participate in the processes of self-inhibition of the less activated glomeruli and of interglomerular inhibition, making it possible to increase the signal-to-noise ratio of the sensory message. The granular cells are depolarized by the glutamate released by the mitral cells. In turn, granular interneurons inhibit mitral cells by releasing GABA, thus forming a negative feedback loop (Shepherd et al., 2007).

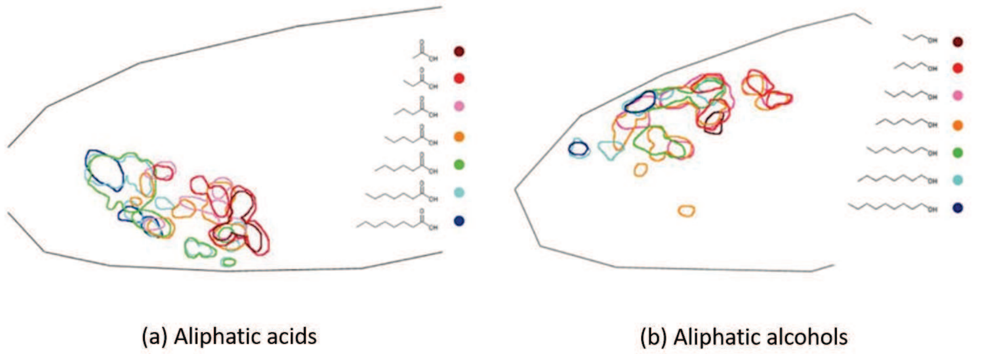
(a) Aliphatic acids (b) Aliphatic alcohols

Figure 7 – Superimposed optical maps of regions in the rat olfactory bulb activated by different chemical compounds: (a) aliphatics acids and (b) aliphatic alcohols. The chemical structure of each odorant is presented to the right, referenced by a specific color (after Uchida et al., 2000).

Granular cells form inhibitory synapses on mitral and tufted cells of multiple glomeruli and mediate interglomerular information transfer (Shepherd et al., 2007; Wilson & Mainen, 2006). In the manner of "bandmasters", these interneurons synchronize the electrical activity of the mitral and tufted cells. They are involved in the processing of information and make the olfactory bulb not a simple relay but a center of integration of the olfactory information.

To visualize the spatial distribution of activity, i.e. the pattern of activated glomeruli compared with those that are not, optical imaging methods have been developed (figure 7). It was thus possible to visualize the olfactory maps in the anesthetized animal during the presentation of odorant molecules (Gurden, Uchida, & Mainen, 2006; Meister & Bonhoeffer, 2001; Rubin & Katz, 1999; Uchida, Takahashi, Tanifuji, & Mori, 2000). However, while natural odors are complex odorant mixtures, studies on the representation of odorant chemistry generally focused on monomolecular odorants (Belluscio & Katz, 2001; Grossman, Mallik, Ross, Kay, & Issa, 2008). The study of spatial maps in response to complex odors remains to be done in detail in the future.

Temporal representation of olfactory responses Concomitantly with spatial coding, the processing of olfactory information also involves temporal coding.

Olfactory information can be represented at different time scales: a slow one, depending on the dynamics of odor sampling (> 100 ms related to respiration) and a faster one, imposed by the oscillatory activity of the network (of the order of ten milliseconds).

As early as the 1940s, Adrian described a slow rhythm in the olfactory bulb and piriform cortex of mammals related to periodic sampling of odorant molecules (Adrian, 1942). The local field potential recordings (summed activity of a large population of neurons and their interactions) show a high amplitude and low frequency oscillation (1-15 Hz) whose variations perfectly follow the modulations of the respiration (Briffaud, Fourcaud-Trocmé, Messaoudi, Buonviso, & Amat, 2012; Gault & Leaton, 1963). These oscillations offer an internal representation of the sensorimotor act of sniffing and also of respiration. It has been suggested that sniffing could filter out ambient odors and amplify the signal of new odors (Verhagen, Wesson, Netoff, White, & Wachowiak, 2007). Despite this, the respiratory patterns of mitral and tufted cells does not represent an odor code by itself, since no specific relationship between an odor and a particular respiratory pattern could be demonstrated until present (Cang & Isaacson, 2003). Furthermore, although a link between odor recognition and the discharge rate of a cell population integrated over the period of respiratory cycle has been observed (Bathellier, Buhl, Accolla, & Carleton, 2008), these results have been questioned when studying these activities on vigilant animals compared to anesthetized. Cury and Uchida (2010) reported that responses of mitral and tufted cells to a temporal scale lower than the respiratory cycle (20-40 ms) were more informative than the rate of discharge measured over an entire respiratory cycle (Cury & Uchida, 2010). Behaviorally, it is now clear that many animals can detect, process, and respond appropriately and differentially to odorants in a few hundred milliseconds. For example, mice are able to respond differentially to odorants within 200 ms when performing a well-learned discrimination task of two odorants (Abraham et al., 2004). Consequently, any use of temporal information for these tasks must be restricted to a small part of the time allocated to the entire task (Leon & Johnson, 2009).

The bulbar network produces rapid oscillations which overlap on this slow oscillation. These oscillations are generated by interactions between mitral and tufted cells and granular interneurons within the olfactory bulb (Neville & Haberly, 2003; Bathellier, Lagier, Faure, & Lledo, 2006). The discovery of the ubiquity of oscillations in the local field potentials of different nerve structures has led the concept of coding by formation of neuron assemblies. These assemblies would be characterized by temporal links uniting the neurons with one another. This coding principle has been demonstrated in locusts (Laurent, 1996). In mammals, such a coding system has so far not been demonstrated. Bulbar processing in mammals is probably more complex because several frequency regimes exist in the oscillatory activity of local field potentials. Indeed, during a respiratory cycle, two fast oscillation regimes overlap the slow oscillation: one in the β band (15-35 Hz) and the other in the γ band (40-80 Hz) (Adrian, 1942). These oscillatory patterns depend on the level of activation of the bulb: they vary with the concentration of the odor or its vapor pressure (Neville & Haberly, 2003; Cenier et al., 2008) and with the air flow in the nose (Courtiol et al., 2011). The synchronization of cells on one of these oscillations would make it possible to select the neurons coding an odor. However, although the neural support for this type of coding exists, no study has yet established the use of such odor coding by the mammalian olfactory system. In their review, Leon and Johnson (2009) even suggest that “the temporal patterns conceivably could arise as an epiphenomenon of lateral inhibition without containing any information that is actually used by the animal”. Thus, although signal synchronization in the olfactory system is probably of great importance, the temporal models studied so far do not seem to explain fully the coding of olfactory information and further studies are still needed to understand these mechanisms.

Upper olfactory centers

Centripetal pathways In higher brain regions, the olfactory information is integrated with information from other sensory modalities, information from past experience, and information concerning the animal’s behavior state, to shape olfactory perception and instruct behavior (Su, Menuz, & Carlson, 2009).

On leaving the olfactory bulb, the axons of the mitral and tufted cells cluster within the lateral olfactory tract to project directly to the primary olfactory cortex. The primary olfactory cortex corresponds to all the regions that receive direct input from the olfactory bulb. These regions include the anterior olfactory nucleus, the olfactory tubercle, the piriform cortex, the cortical nucleus of the amygdala and the entorhinal cortex (Carmichael, Clugnet, & Price, 1994; de Olmos, Hardy, & Heimer, 1978; Turner, Gupta, & Mishkin, 1978). Unlike all other sensory modalities, these projections are characterized by the absence of thalamic relay between the periphery and the cortex. Nevertheless, olfactory information is ultimately relayed through the thalamus to the neocortex (Price, 1973).

Each of these cortical subregions addresses information to different areas of the brain (Haberly, 2001; Lledo, Gheusi, & Vincent, 2005): the olfactory nucleus anterior to the ipsilateral and contralateral piriform cortex; the olfactory tubercle in the medial dorsal nucleus of the thalamus, which in turn projects to the orbitofrontal cortex, the region thought to be involved in the conscious perception of smell (Rolls, 2001); the piriform cortex is also projected into the medial dorsal nucleus of the thalamus; it also has direct connections to part of the orbitofrontal cortex and the insular cortex. This projection in the neocortex is involved in olfactory perception and discrimination (Savic, Gulyas, Larsson, & Roland, 2000). The entorhinal cortex projects mainly into the hippocampus. Finally, the amygdala is projected mainly in the hypothalamus. All of these areas (except the olfactory tubercle) establish reciprocal connections with the olfactory bulb (figure 8).

Thus, the cortical organization of the olfactory centers differs from the other senses in different ways. The first aspect is the direct projection of second-order sensory neurons on the cortex, without thalamic relay. The second aspect is the large number of centrifugal connections that return from the cortex to the previous level of treatment, the olfactory bulb. Finally, the third aspect is its close relationship with the amygdala and the entorhinal cortex. Indeed, the amygdala is the gateway for emotions essential in the perception and emotional memory observed in humans (Dolan, 2002). The lateral entorhinal cortex is closely related to the hippocampus and represents a key structure in the encoding and recall of many forms of declarative memory (Eichenbaum, 2001). In other sensory modalities, the limbic system is reached only after multiple cortical relays

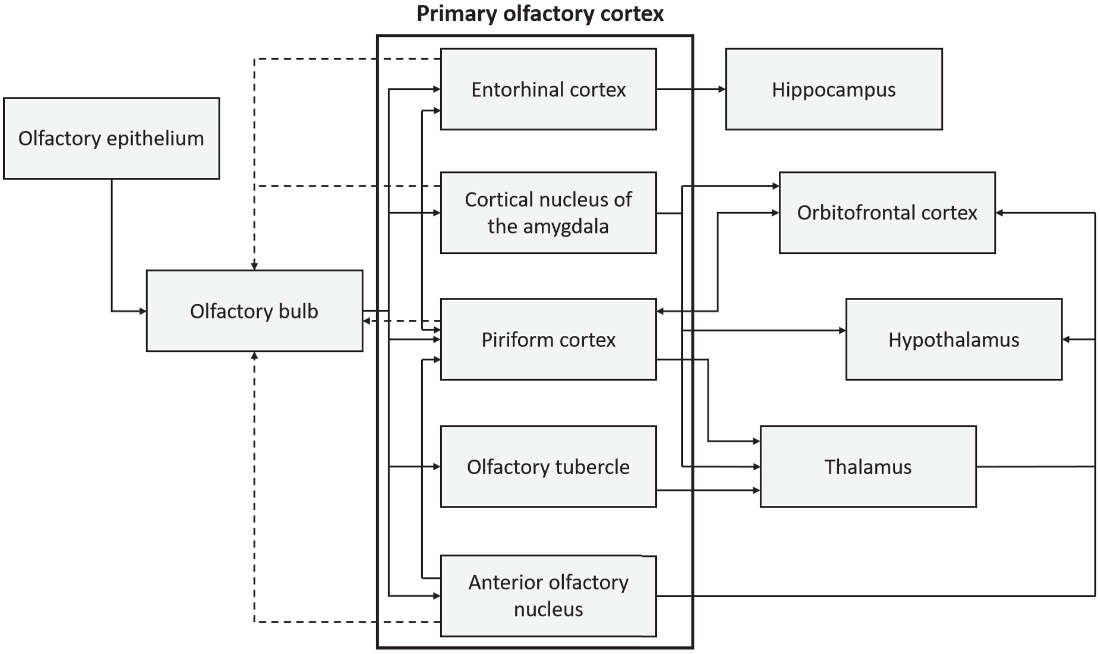

Figure 8 – Main structures and connections of the olfactory system of vertebrates. Solid arrows represent the centripetal pathways and the dotted arrows represent the centrifugal pathways.

in high-level associative regions (Turner, Mishkin, & Knapp, 1980) and after passage through the thalamus, the site of sensory integration. These specificities, which are relative to the olfactory system, contribute to the very strong link that exists between olfaction, emotion and memory.

Centrifugal pathways Odor perception is not a simple feedforward process in mammals: there is also a "top-down," or centrifugal pathway that provides feedback and other forms of regulation. Ultimately, odor perception is shaped by the interaction of the two pathways. The regulation of the olfactory bulb is mediated by cortical returns on the one hand and neuromodulatory afferents on the other hand. It allows the olfactory bulb to modulate its activity according to contingencies related to olfactory learning or the internal and external context (internal state of the animal, experimental conditions, environment) (reviewed by Rinberg & Gelperin, 2006).

All regions innervated by the olfactory bulb, except the olfactory tubercle, send in return olfactory centrifugal projections. These cortical returns come mainly from the piriform cortex and the anterior olfactory nucleus. They mainly target the granule cells but also the periglomerular cells of the olfactory bulb, without any medio-lateral regionalization (Matsutani, 2010). These cortical returns are glutamatergic and allow an excitation of these cells leading to a facilitation of the auto-inhibition of the mitral cells (Balu & Strowbridge, 2007; Strowbridge, 2009).

Moreover, the cellular actors of the olfactory bulb express a large panel of receptors to different peripheral and central neuromodulators. The olfactory bulb has the characteristic of receiving, among the four usually encountered, only three types of neuromodulatory fibers: cholinergic, noradrenergic and serotoninergic fibers. Overall, these three neuromodulatory systems act primarily within the olfactory bulb by modulating the balance between excitation and inhibition of olfactory bulb cell activity. This modulation would help to sculpt the odor response according to the animal's state of alertness and level of attention (Chaudhury, Escanilla, & Linster, 2009; Linster, Nai, & Ennis, 2011; McLean, Darby-King, & Hodge, 1996). The centrifugal neuromodulatory fibers have been suggested to influence odor discrimination, provide a means of gain control and generate local experience- dependent changes in the olfactory bulb. It will be particularly interesting to learn more about the mechanisms through which these fibers are activated (Su et al., 2009).

Animal model: the house mouse, *Mus musculus domesticus*

Life history of the house mouse

The house mouse, *Mus musculus domesticus*, a subspecies (box 3) from the *Mus musculus* complex, originates from South-West Asia (Suzuki et al., 2013). House mice would have become commensal during the initial settlements of humans in the Middle East during the Neolithic, presumably ever since humans were able to exploit stored grains (Jones, Eager, Gabriel, Jóhannesdóttir, & Searle, 2013; Cucchi, Auffray, & Vigne, 2012). The distribution range of *M. m. domesticus* then expanded, probably thanks to increasing human trade, around the Mediterranean Sea during the Iron Age (Cucchi et al., 2012). The subspecies subsequently spread to North-West Europe during the Viking era, and then to much of the rest of the world following the Age of Discovery (figure 9) (Jones et al., 2013). Nowadays, *M. m. domesticus* is cosmopolitan, being present in western Europe, Africa, North and South America, Australasia and numerous oceanic islands.

Its large dispersion throughout the world has been possible thanks to its high adaptability, particularly to human environments. This nocturnal animal occupies all forms of human habitat, from buildings of large agglomerations to agricultural buildings, warehouses and even high altitude refuges. If the environment and conditions are favorable, mice can breed for most of the year, with low intensity during the winter. Its ecological success involves drastic changes of its food repertoire in order to utilize locally available resources. House mice are dietary generalists with a predominantly granivorous diet which exploits a large variety of food resources, usually supplied to farm animals or stored for human consumption (Berry, 1970).

These characteristics facilitate common exposure to new food items, some of them potentially dangerous and make it an excellent model for the study of social transmission of food preference.

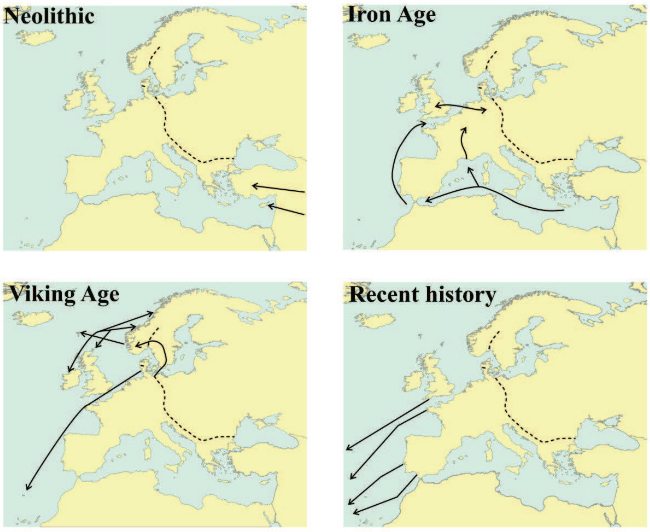

Figure 9 – Maps showing the different possible colonization pathways taken by the house mouse, *Mus musculus domesticus*, based on mitochondrial DNA evidence. The dashed line shows the location of the hybrid zone between the subspecies *M. m. domesticus* and *M. m. musculus* (after Gabriel et al., 2010).

Box 3. *Domesticus*: species or subspecies?

Begun on the basis of morphological comparisons made by Schwarz and Schwarz (1943), the systematic of the *Mus musculus* complex was clarified later with the advent of molecular and biochemical tools (Schwarz & Schwarz, 1943). It was nowadays well established that commensal and aboriginal groups of mice form two separate lineages within the *Mus musculus* complex.

If an agreement was found for the three taxa of aboriginal mice (*M. spretus*, *M. spicilegus* and *M. macedonicus*), there is still no agreement on the best way to classify the house mouse. Some authorities treat *musculus* and *domesticus* as subspecies or semispecies of *musculus* (e.g. Thaler, Bonhomme, & Britton-Davidian, 1981) whilst others regard them as distinct species (Sage, Atchley, & Capanna, 1993).

In 1990, the International Commission for Zoological Nomenclature have established that the name *domesticus* is legitimate, and is available for use either as *Mus domesticus* or as *Mus musculus domesticus*.

Social organization of the house mouse

In natural conditions, house mice (figure 10) are highly social species that form complex social systems with a flexible structure, often dependent on the distribution of food resources (Noyes, Barrett, & Taylor, 1982) and the physical complexity of the environment (Bronson, 1979). Generally, they form social groups, consisting of a dominant male, one or several adult females with their young and several subordinate mice of both sexes living on an exclusive territory (König & Lindholm, 2012; Hurst, 1987; Bronson, 1979; Lidicker, 1976; Singleton, 1983).

Figure 10 – Two adults house mice, *Mus musculus domesticus*, consuming an ear of corn. ©CC0 Creative Commons

This species is characterized by a polygynous mating system and a male-biased dispersal (Gerlach, 1996). The young males generally disperse under the pressure of adults (aggression of territorial males in particular). Females often remain in their natal territory but occasionally disperse and successfully immigrate into other breeding units where they encounter unrelated and unfamiliar same-sex conspecifics (box 4). Generally, females move more easily from one group to another than males (Bronson, 1979; Anderson & Hill, 1965; Berry, 1970; Baker, 1981; Gerlach, 1990; Pocock, Hauffe, & Searle, 2005).

Both the dominant male and breeding females aggressively defend their territories against neighbors and unfamiliar intruders (Rowe & Redfern, 1969;

Hurst, 1990a, 1990b, 1990c; Latham & Mason, 2004). Territorial males spend most of their time within their own territory and defend their access to females and other resources. They are particularly intolerant toward other male intruders (Bronson, 1979; Crowcroft & Rowe, 1963; Palanza, Mainardi, Brain, Re, & Parmigiani, 1996). Their success in excluding intruders and their tolerance of subordinate males living within the social group varies widely and depends on other elements such as the physical structure of the habitat or the density of the population (Reimer & Petras, 1967; Lidicker, 1976; Hurst, 1987; Drickamer, Gowaty, & Holmes, 2000).

Box 4. Notions of familiarity and relatedness

In general, the *degree of relatedness* corresponds to the relationship of genetic proximity shared with another individual. *Familiarity*, for its part, is dependent on the social interactions between two individuals and represents the physical and temporal proximity shared with another individual.

In the context of this manuscript, two animals are considered to be related if they have at least one grand-parent in common. In addition, two individuals are considered familiar when they belong to the same social group.

Under laboratory conditions, familiarity requires that individuals share the same environment. Because of the social intolerance that exists between unfamiliar individuals of this species, the procedure of our laboratory is to train social groups from an early age to ensure their stability. One week after weaning, the mice are then placed in same-sex sibling groups.

As a result, in our experimental conditions, familiarity and relatedness between individuals are confounded. In the remainder of this manuscript, when the term *familiar* is used in the context of our experimental conditions, it will systematically imply that individuals are also related. Similarly, when the conspecifics are considered as *unfamiliar*, they are also unrelated.

These conditions, particularly in the case of females, reflect the natural conditions observed generally in this species.

Female house mice display sexual preferences for dominant males (Drickamer, 1992) and compete with other females over access to mates and resources availability (such as food resources and nest sites). The frequency of agonistic behavior involving females is low in comparison with those between males and is often related to pregnancy and lactation (Hurst, 1987; Brain & Parmigiani, 1990). They also cooperate with one another by developing a communal nesting and nursing system such as babysitting, social thermoregulation, or defense of pups. The most glaring example of cooperation in this species is the case where two females (or, rarely, more) share their litter in a common nest and care indifferently for all the pups present in the nest (reviewed by König & Lindholm, 2012). This association allows a better reproductive success (König, 1989), probably by limiting infanticide (Manning, Dewsbury, Wakeland, & Potts, 1995) and by improving the growth of pups thanks to the increase of milk production of females (Wilkinson & Baker, 1988; Konig, 1993). Spatial proximity and nest sharing generally precede reproductive associations in house mice (Manning et al., 1995; Rusu & Krackow, 2004). In natural and semi-natural populations, female house mice associate spatially and most commonly nest with related females (Wilkinson & Baker, 1988; Dobson, Jacquot, & Baudoin, 2000; Rusu, König, & Krackow, 2004). Indeed, familiarity during the development of young females (as is the case with siblings) is important for such social interactions (König, 1994).

Finally, male-female interactions are also characterized by a low frequency of agonistic behavior in relation to odor cues communication (reviewed by Hurst, 1990c). The male-female bonding in a social group is quite weak in this species and several behavioral observations indicate that female house mice are actively polyandrous and will mate with both dominant and subordinate males (Rolland, MacDonald, De Fraipont, & Berdoy, 2003). The frequency of multiple mating was estimated to be 45-70% and mixed paternity in litters from natural populations of house mice has been shown to be approximately 23% (Thonhauser, Thoß, Musolf, Klaus, & Penn, 2014; Dean, Ardlie, & Nachman, 2006).

The establishment and maintenance of this social system is possible because house mice mainly use olfactory communication with in particular the deposit of olfactory marks (i.e. feces, urine) in their environment. Communication through olfactory marks is essential for territory defence, modulation of social status within social groups and sexual communication (Hurst, 1990a, 1990b, 1990c). For example, this information serve to individual identification and familiar individuals can recognize each other after a separation period of at least seven days (Hurst, 1990a; Nevison, Armstrong, Beynon, Humphries, & Hurst, 2003; D' Amato & Moles, 2001).

Thesis objective

Although animal food choices may be affected by internal factors and personal experience, the social component may also play a major role in animal feeding strategies. Among the social influences observed in the animal world, the social transmission of food preference (STFP) is a mechanism that could allow rodents to enlarge their food repertoire at lower risk. Many studies in laboratory animals have made it possible to understand the major mechanism of this social influence and the robustness of direct STFP in rodents. However, few studies have focused on the functional conditions under which the STFP could be effective, especially in the case of the indirect STFP.

The objective of this project is to determine how mice use their social olfactory environment to make food choices. By using a mouse model of wild origin (box 5), I tried to get a better understanding of the conditions in which the STFP, by direct or indirect ways, can be used by the house mouse.

The use by mice of two ways of STFP supported by the same underlying neurobiological mechanism has led to the question: do they have different advantages and limitations for mice? Indeed, direct and indirect STFP present the information characterizing a new food source in very different social contexts. As a result, the conditions required to establish the STFP can vary considerably between these two pathways.

This thesis work is organized around three main questions to which three chapters provide elements of response.

In *Chapter 1*, I wonder whether the social constraints of the house mouse could affect the establishment of direct and indirect STFP. Given the description of the social organization of the house mouse in natural conditions, individuals are expected to exchange social information primarily within their social group. However, because different foods are not randomly distributed in space, mice from a given group should tend to have similar food sources whereas mice from different social groups should differ in their diet at a larger scale. Consequently, gathering information about food from unfamiliar conspecifics could help enlarging the food repertoire of the individuals. However, given the social constraints that exist in this species, learning from unfamiliar individuals is not an easy task and the social intolerance between two unfamiliar individuals could provide a real limit of the STFP. One of the key differences between direct and indirect STFP is the presence or absence of the conspecific when acquiring information. This difference could play a major role in the acquisition of information from unfamiliar conspecifics. Thus, I propose, in this chapter, to evaluate the effect of the unfamiliarity of the information provider on the efficiency of the direct and indirect STFP. Because of the constraint of a social contact, I suspect that the direct STFP should be inefficient between unfamiliar mice whereas indirect STFP should be effective.

Box 5. The importance of studying house mice of wild origin

Although studies on laboratory mice and rats have been extremely useful for understanding how the social transmission of food preference (STFP) occurs in rodents, it is unclear whether these findings can be extrapolated to wild animals and how that could be done. First, domesticated, laboratory strains kept in conventional conditions present significant differences in their behavior and physiology compared to wild individuals (Crawley et al., 1997). This can affect elements such as social intolerance between unfamiliar individuals and do not reflect constraints observed in natural conditions (E. O. Price, 1999). Second, natural selection maintains genetic diversity in natural populations and the genetic background of animals can affect information characterizing the individual and thus indirectly the decision-making processes of individuals perceiving this information. So, it seems difficult to generalize results in laboratory strains without testing wild animals. On the other hand, laboratory conditions greatly facilitate the study of nocturnal species such as the house mouse and allow both to study precise parameters and to control the observation conditions.

For these reasons, the study of STFP in house mice of wild origin seems like a good compromise between these two experimental conditions. It provides a more detailed analysis of food strategies developed by rodents and improves the understanding of this social behavior under natural conditions.

One of the major challenges of this thesis is also to deepen the knowledge about indirect STFP. Thus, in *Chapter 2*, I decided to evaluate the necessary conditions for the establishment of the indirect STFP. Another difference that exists between direct and indirect STFP is the information collected about diet by mice. For the direct STFP, the odour of the new diet comes from the breath or food scraps present on the conspecific and should not differ from the odor of the diet itself. For the indirect STFP, before reaching feces of an individual, the diet that was consumed underwent a passage through the digestive system. The risk of molecule degradation or absorption caused by the digestive process could affect the matching between diet odor perceived from the conspecific and the odor of the diet itself and consequently prevent the indirect STFP. I, thus, propose in this chapter to evaluate the efficiency of foods differing in their capacity to be a good support for indirect STFP in house mice. Because the absorption or degradation of molecules during the digestive process depends in part on their molecular structure, I expect that the acquisition of indirect STFP would depend on the multiplicity of the odorant molecules present inside the diet.

Finally, in *Chapter 3*, I wonder whether the simultaneous perception of multiple information in olfactory marks could lead to competition between social and food information during the acquisition of indirect STFP and affect the conditions under which this social influence would be functional. Olfactory marks such as urine and feces provide, in rodents, rich information about the characteristics of the donor, in addition to information about new food sources. This type of information may be relevant to mice, particularly as part of their breeding strategies. In this case, the competition between social information and food information may be different depending on the sex of the individuals who perceive them. Thus, I propose, in this chapter, to evaluate the efficiency of the indirect STFP in male and female mice by varying the characteristics of the donors. Given the breeding strategies of this species, I expect females to prioritize food information while males prioritize social information.

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Chapter 1

Transmission of food preference between unfamiliar house mice is dependent on social context

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Transmission of food preference between unfamiliar house mice (*Mus musculus domesticus*) is dependent on social context

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Acknowledgments

We gratefully thank Isabella Clegg and Heiko G. Rödel for the revision of the English and Jean-Luc Durand for statistical advices. We also gratefully thank the three anonymous reviewers for their constructive suggestions which helped to improve our manuscript.

Accepted in *Journal of Comparative Psychology* ©2018, American Psychological Association.

Abstract

Rodents obtain information about a new food source through olfactory cues of conspecifics and consequently develop an attraction for this diet. Generally, physical contact between an observer and a demonstrator that has recently consumed a novel food item is required to allow the social transmission of food preference (STFP). However, in natural populations of house mice, social encounters between unfamiliar individuals usually turn into a fight. Thus, social intolerance between the individuals involved could prevent STFP. It has been shown that the feces of rodents can act as a social stimulus and promote STFP in mice, which could reduce the social constraints associated with an encounter. Here we examined the acquisition of the STFP in female house mice of wild origin (*Mus musculus domesticus*) after a direct encounter with a familiar and unfamiliar female, and after the presentation of olfactory marks of an unfamiliar female. Unlike in encounters between familiar females, our results did not provide significant support for the existence of STFP after encounters between two unfamiliar females, independently of the occurrence or absence of offensive agonistic behavior. However, STFP through olfactory marks of an unfamiliar female was effective. We suggest that the social context might strongly impair direct STFP, not necessarily via the unfamiliarity of the information provider but rather via its physical presence.

Keywords: familiarity, olfactory communication, stressful context, wild origin

Introduction

Animals can acquire information on challenging environments using trial-and-error tactics or by interacting with others and observing their coping responses (Galef & Giraldeau, 2001). Benefits of using social information consist in reducing costs related to learning strategies by trial and error and in providing additional information with respect to personal information. As a consequence, using social information may allow a more accurate estimate of current environmental conditions (Doligez et al., 2003).

The use of social information, however, does not necessarily enhance the fitness of the individual. Because familiar conspecifics are more likely than stranger individuals to share genes or environments with an individual, “friend copying” should be a superior strategy for copying than copying with unfamiliar individuals (Laland, 2004; Kendal, Coolen, van Bergen, & Laland, 2005). However, in some cases, the unfamiliar individual may represent a relevant and sometimes richer source of information than a familiar individual. Individuals from the same social group tend to forage in the same feeding sites and therefore share similar diets (Galef & Clark, 1971; Gerrish & Alberts, 1995). In this case, an unfamiliar individual could then have acquired a different food repertoire and thus could provide information with the potential to improve the fitness of an individual.

The social transmission of food preference (STFP) has been studied in rodents for several decades. Under natural conditions, it was suggested that rodents enlarge their food repertoire at low risk by getting information on novel food sources from experienced conspecifics (Galef, 1986). Following a social encounter with a conspecific demonstrator that has recently consumed a novel food item, rodents such as rats and mice will subsequently show a substantially enhanced preference for the same food source as ingested by their demonstrator (Galef & Wigmore, 1983; Posadas-Andrews & Roper, 1983; Valsecchi & Galef, 1989).

As proposed by Coussi-Korbel and Fragaszy (1995) for nonhuman primates, the amount of information that a naive animal acquires when interacting with a conspecific can be determined by the characteristic of interactions between individuals. Such social influence on rodent STFP has been tested in previous studies exploring the effects of familiarity and kinship (Choleris et al., 1997; Choleris et al., 1998; Galef & Whiskin, 2008; Valsecchi et al., 1996).

In a laboratory study with Long-Evans rats (*Rattus norvegicus*), Galef and Whiskin (2008) showed that an unfamiliar female demonstrator had a stronger influence than a familiar female demonstrator on the food choices of naïve female observers, suggesting that information from unfamiliar conspecifics can outweigh the relevance of information from familiar ones. In such conditions, the observers spent less time interacting with the familiar demonstrator than with the unfamiliar one, which can be explained by the novelty aspect of the unfamiliar conspecific. The time spent interacting with the familiar demonstrator was, nevertheless, sufficient to allow an STFP. The authors suggested that interacting with the familiar demonstrator was less stimulating than interacting with the unfamiliar one, which could have promoted the learning process regarding food preferences (Galef & Whiskin, 2008). However, domestication of rats and mice resulted in selecting individuals with high levels of tolerance to conspecifics (Price, 1999). In wild house mice, encounters between unfamiliar animals usually turn into a fight and they tend to avoid each other (Crowcroft & Rowe, 1963; Hurst, 1987). This high difference in social tolerance between wild and laboratory animals could greatly impact the efficiency of the STFP from unfamiliar conspecifics in natural conditions. The use of social information would be severely impaired by insufficient durations of the social contact, or alternatively, by socially stressful contexts. Indeed, according to Sandi and Pinelo-Nava (2007) the effect of stress on memory follows an inverted U-shape: a certain amount of stress is known to favor learning processes whereas a highly stressful situation will preclude it (van der Kooij & Sandi, 2012). This hypothesis has been supported in adult Mongolian gerbils (*Meriones unguiculatus*) in which "socially induced anxiety may interfere with the acquisition of a food preference from an unfamiliar/unrelated conspecific" (Choleris et al., 1998; Valsecchi et al., 1996).

In a first experiment, we evaluated in female house mice (*Mus musculus domesticus*) of wild origin the acquisition of STFP after direct interaction with a familiar and an unfamiliar demonstrator. Experimental conditions followed previous studies conducted with laboratory rodents (Arakawa et al., 2013; Galef & Wigmore, 1983; Posadas-Andrews & Roper, 1983; Valsecchi & Galef, 1989). We hypothesized that the high level of social intolerance during an encounter between unfamiliar mice of wild origin should prevent the STFP.

Mice can also obtain information from conspecifics without direct interactions with them. Olfactory marks left by mice constitute relevant sources of information (Laland & Plotkin, 1991), as body odors, urine and feces convey numerous olfactory cues about traits (e.g. identity, sex, and species) and states (i.e. diet, age, health condition) of individuals (Colombelli-Négrel & Gouat, 2006; Ferkin et al., 1997; Hurst et al., 2001; Osada et al., 2003). During a direct encounter, a key volatile element necessary to the establishment of a food preference in the observer is carbon disulfide (CS_2) contained in the breath of the demonstrator (Galef, 1988; Valsecchi & Galef, 1989). The neurobiological cascade promoting the STFP is the consequence of the simultaneous perception of carbon disulfide and of the new food odor. The underlying mechanism has been described in details and the specific receptor of carbon disulfide has been identified (Munger et al., 2010). The guanylyl cyclase receptor responding to carbon disulfide also responds to uroguanylin, a peptide present in the urine and feces of rodents. This peptide acts as a social stimulus in the same way as carbon disulfide and it has been shown that feces were able to promote STFP in laboratory mice (Arakawa et al., 2013). Gathering social information indirectly via olfactory marks is less risky and would be less stressful than following direct contact with conspecifics.

In a second experiment, in order to enhance the conditions for an efficient STFP between unfamiliar females, we used diets contrasting more in their constitutive elements, and assessed the acquisition of the STFP between unfamiliar conspecifics after direct interactions and through indirect communication. Under the conditions of indirect communication, because mice acquire the information from olfactory marks without a direct interaction with the unfamiliar demonstrator, we would expect STFP to take place.

Materials and Method

Animals and breeding conditions

The animals used in this study were house mice, *Mus musculus domesticus*, descendants from animals of wild origin provided and bred for more than ten generations at the laboratory RS2GP of VetAgro Sup Lyon (France). The mice were bred in our laboratory for seven generations with addition of wild animals captured at different sites in France, in the Die region (Vachères en Quint 44.789720 N, 5.259654 E, Montlaur en Diois 44.789720 N, 5.259654 E) and in the Beaujolais region (Chambost-Allières 46.012944 N, 4.481324 E).

Given the high levels of aggression between males, which typically escalates rapidly (Patris, Gouat, Jacquot, Christophe, & Baudoin, 2002); we only tested our hypotheses in females for ethical reasons. We used 155 adult females (M_{age}= 151 d, $SEM = 4$, 95% CI [143, 160]).

The room in which the mice resided was environmentally controlled on a 14:10-h-light-dark cycle (19:00-9:00-h lighting) at a temperature of 20 ± 2 °C and relative humidity of 50-60%. During the dark phase, the room was lit by a red light (two neon tubes, 35 W) allowing observation by the experimenter. The mice were housed in standard polycarbonate cages (26×14 cm and 16 cm high) with a bedding of wood shavings (Special Diet Services, Witham, Essex, U.K.) and cotton as nesting material. Pelleted food (type M20, Special Diet Services, Witham, Essex, U.K.) and water were supplied *ad libitum*. The mice were weaned at 21 days of age and were placed in same-sex sibling groups one week later. At least one week before the experiment, animals were transferred to the experimental room. Females were placed in a new cage with same-sex siblings (in groups of two) but they were tested individually. Individuals were individually marked by hair clipping when necessary.

Diets

Diets used in these experiments derived from baits originally designed to control rodent pest populations. The diets were specifically manufactured for these experiments by Liphatech (Liphatech S.A., Pont du Casse, Lot et Garonne, France) and did not contain any rodenticide.

In *Experiment 1* (see details below), the two diets were of the same composition and only differed by the addition of a single odorant molecule: either 0.1% of cinnamaldehyde (referred to as “cinnamaldehyde diet” hereafter) or 0.1% of eugenol (referred to as “eugenol diet” hereafter). The bait used was an artificial paste with high lipid content.

In *Experiment 2* (see details below), the two diets were of different nature in order to increase the contrast between components with the goal of facilitating the acquisition of social transmission of food preference (STFP). One diet was the artificial paste described previously without the addition of odorant molecules (referred to as “paste diet” hereafter) and the other diet was composed of oat grains with a red coating (referred to as “oat diet” hereafter).

Experimental procedure

The general paradigm used in this study was based on the different procedures developed to test the STFP in rats and mice where each experiment encompassed a social phase followed by a choice test (Arakawa et al., 2013; Galef & Wigmore, 1983; Posadas-Andrews & Roper, 1983; Valsecchi & Galef, 1989). During the social phase, a naïve observer was confronted with social information about a given diet through a direct encounter with a demonstrator or through the presentation of the olfactory marks of a conspecific donor. Each experiment included two groups of animals differing in the nature of the diet experienced by the demonstrator or the donor. During the choice test, the observer was confronted with the two diets. The STFP was considered as being acquired when the two groups differed significantly in their food preference.

Social phase

Direct STFP

Experiment 1 Prior to the dyadic encounter and during the dark period, the demonstrator was placed in a clean standard polycarbonate cage for 45 min and was given 2 g of cinnamaldehyde diet or eugenol diet. At the end of this period, the consumption of the diet was quantified, respectively (cinnamaldehyde diet: $M_{consumption\ per\ individual}$= 0.20 g, SEM = 0.04, 95% CI [0.12, 0.27]; eugenol diet: $M_{consumption\ per\ individual}$= 0.22 g, SEM = 0.04, 95% CI [0.13, 0.31]). The demonstrator was then placed in a similar clean cage divided in two equal parts by a Plexiglas wall. Each compartment contained one cardboard tube to serve as a shelter and to prevent recurrent chases. The observer was placed in the other compartment of the cage. A transparent tray was placed on the cage to prevent observers from escaping, and to allow observation and video recording (Sony FDR-AX100E). The dyadic encounter lasted 15 min beginning with the removal of the Plexiglas wall but could be stopped in case of escalated fighting (see ethics note below). At the end of the dyadic encounter, the observer was transferred to a clean test cage and the demonstrator was returned to its home cage. The choice test (see below) started five min after the time allocated to the dyadic encounter (15 min), even when the dyadic encounter had to be stopped. 32 females (from 10 breeding pairs) were used as observers, 16 additional females (from 9 breeding pairs) were used both as familiar and related demonstrators with 16 observers and as unfamiliar and unrelated demonstrators for the remaining 16 observers. All the females were kept in pairs. Mice from a same pair, whatever demonstrator or observer, were used in the same day, one after the other, to avoid any bias due to social communication with their partner when they were returned to their home cage.

Experiment 2 The procedure was the same as that described for *Experiment 1*. The consumption of the diets was quantified (oat diet: $M_{\text{consumption per individual}}$= 0.11 g, SEM = 0.02, 95% CI [0.07, 0.15]; paste diet: $M_{\text{consumption per individual}}$= 0.22 g, SEM = 0.05, 95% CI [0.12, 0.32]). Four demonstrators (two in oat group and two in paste group) did not consume the proposed diet and observers which interact with them during the social phase were removed from the experiment with their respective observers. In total, 44 females (from 17 breeding pairs) were used as observers and 44 females (from 17 breeding pairs) of which 15 were used in *Experiment 1*, unfamiliar and unrelated with observers, served as demonstrators.

Indirect STFP Donors were given 3 g per day and per individual of one of the two diets simultaneously with the standard diet during three days. The consumption of the diet was quantified at the end of this period (oat diet: $M_{\text{consumption per individual}} = 6.86$ g, $SEM = 0.50$, 95% CI [5.88, 7.84]; paste diet: $M_{\text{consumption per individual}} = 8.88$ g, $SEM = 0.13$, 95% CI [8.63, 9.12]). The olfactory marks of donors were collected during the lit period by gently rubbing the anogenital area of the donor with the lid of a Petri dish (3.5 cm in diameter) for 10 s. Each sample was placed in a sealed freezer bag and placed at −80 °C until required. On the day of the experiment, the Petri dish carrying olfactory marks of the donor was thawed 30 min before the beginning of the social phase. It was placed on a support (figure 1.1) together with a clean Petri dish (control) to verify that the observer perceived the odorant stimulus (Colombelli-Négrel & Gouat, 2006). The position of each dish on the support (left/right) was randomly assigned and balanced across trials. The social phase occurred during the dark period. The observer was placed in a clean cage covered by a transparent tray and had five min to acclimate to the cage. The support with the dishes was introduced into the cage. The presentation of the olfactory marks lasted five min starting with the first contact of the mouse with the support. Investigation time of each dish was measured from a video-recording of the experiment. At the end of the social phase, the support and the Petri dishes were removed and the observer was transferred to a clean test cage. The choice test (see below) began five min later. 22 females served as observers (from eight breeding pairs), 12 additional females (from nine breeding pairs) were donors and were all unfamiliar and unrelated with their respective observers.

Choice test

For both experiments, the procedure of choice test was the same. A 3 g sample of each diet was placed in a Petri dish to limit the dispersion of unconsumed food. The two Petri dishes were fixed to a support of the same type as the one shown in the figure 1.1 and then placed inside the test cage. The position (left/right) of each diet was randomly assigned and balanced across trials. A transparent tray was placed on the cage to prevent observers from escaping, and to allow

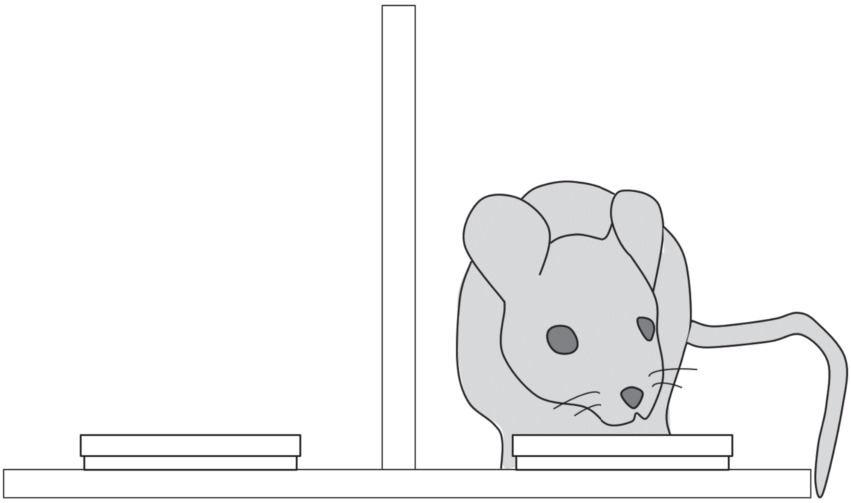

Figure 1.1 – Sketch of the device presenting a Petri dish including the olfactory marks of a donor and a clean Petri dish (control), with a mouse investigating the dish on the left side.

observation. The support with the diets was introduced into the test cage and the test began from the first contact of the mouse with the support. When the test was finished at 10 min, the observer was returned to its home cage. When it was extended to 1 hr, the observer was left in the experimental cage and the diets were therefore reintroduced into the cage after weighing. The remaining food was collected carefully inside the cage and the amount of unconsumed food was weighed to the nearest 0.02 g using a digital balance. In *Experiment 2*, the choice test was video recorded during the first 10 min and the consumption time of each diet was measured.

The duration of the choice tests differed between the two experiments (*Experiment 1*: 10 min and 1 hr; *Experiment 2*: 10 min) and was much shorter than the test duration (24 hr) used in many previous studies (Galef & Whiskin, 2008; Valsecchi & Galef, 1989). However, a short duration had already been used in other studies (Arakawa et al., 2013; Ervin, Mulvale, Gallagher, Roussel, & Choleris, 2015; Posadas-Andrews & Roper, 1983) and appeared more appropriate to reflect feeding in natural conditions.

Ethics note

Experimental procedures were approved by the French ethics committee "Charles Darwin C2EA 05" (reference number 04355.02). During all social encounters, the experimenter monitored the animals constantly and encounter was interrupted when the endpoint was reached (i.e. more than three successive roll-over fights or chases with bite). This study did not require euthanasia of mice at the end of experiments and subjects were therefore retained for later use.

Data analysis

The data collection and analysis were done blind to group identity to remove any source of unintentional bias. Because of the small number of animals in each group ($N < 30$), we used non parametric statistics. The results are reported by their mean (M), standard error (SEM) and confidence intervals (CI) (level of confidence: 95%). When the comparison of two sample means was significant ($p \leq .050$), we also reported the effect size by using the Cohen's d value. All statistical comparisons were performed with the software StatXact (Cytel Software Corporation, 2010).

In *Experiment 1*, the acquisition of the STFP was assessed by comparing the proportion of cinnamaldehyde diet consumed by the observers of the two experimental groups (cinnamaldehyde group vs. eugenol group) during the choice test (Galef & Wigmore, 1983). The proportion of cinnamaldehyde diet corresponded to the ratio of the quantity of cinnamaldehyde diet consumed over the total consumption (total quantity consumed) of both diets. In *Experiment 2*, the acquisition of the STFP was assessed by comparing the proportion of oat diet consumed by the observers of the two experimental groups (oat group vs. paste group) during the choice test. When an observer did not consume any diet during the choice test, it was removed from analysis. We used Fisher Pitman permutation tests for independent samples.

In *Experiment 2*, we also expected that when mice have perceived information about a new diet, they should consume this new food source with more confidence. We then compared the speed of consumption of each diet (amount of consumed diet / consumption time) expressed in $\mathrm{mg\,s^{-1}}$, between the two experimental groups for each diet independently. Only individuals that have consumed the given diet were included in the analyses and Fisher Pitman permutation tests for independent samples were used.

Direct social encounters between unfamiliar conspecifics in wild house mice, which usually turn into a fight (Hurst, 1987), could cause high levels of stress and strongly limit proximity, and therefore olfactory communication, between the two females. Thus, for each procedure involving direct encounters, we quantified the duration of occurrences of investigative behavior of the mouth area of the demonstrator (nose to nose, mouth to mouth, facial investigation) expressed by observers and the frequency of occurrence of offensive agonistic behavior (attack, bite, chase, roll-over fight) expressed by observers and demonstrators (cf. Clipperton et al., 2008; Grant & Mackintosh, 1963; Patris et al., 2002). We hypothesized that a high level of aggression during the dyadic encounters should reduce duration of the social investigative behavior between individuals and thus preclude the STFP. In order to test this hypothesis, observers were divided into two groups according to the presence or absence of offensive agonistic behavior during the encounter. The duration of investigative behavior of the demonstrator's mouth area expressed by observers was compared between these two groups. To compare the acquisition of the STFP between these two groups despite the demonstrator's diet, we estimated an index of diet preference based on the proportion of demonstrator's diet consumed. This index is equal to $(D/(D+O))$ where D represents the quantity of the diet matching with the demonstrator's diet and O represents the quantity of the other diet consumed. We used Fisher Pitman permutation tests for independent samples with stratification by the demonstrator's diet.

For indirect STFP, to verify the interest of the observers for the olfactory marks presented during the social phase, we compared the duration of investigative behavior expressed by observers for each dish present on the device (figure 1.1). For this, we used Fisher Pitman permutation tests for paired samples. We also hypothesized that the duration of the investigative behavior expressed by observers during the social phase could affect the acquisition of the STFP. By using Spearman's rank correlation, we tested for associations between the investigating time expressed by the observers on the Petri dish carrying olfactory marks of the donor and their index of diet preference.

Results

Experiment 1

Familiar females

One of the 16 tests was removed from the analyses because the observer presented an abnormal repetitive behavior during the experiment (Garner, 2005).

Social phase We did not observe any agonistic interactions during encounters of familiar females. All observers investigated the mouth area of their demonstrator ($M_{\text{duration}} = 28$ s, $SEM = 3$, 95% CI [22, 34], $N = 15$), i.e. all observers potentially had the opportunity obtain olfactory information related to the diet of the demonstrator.

Choice test During a choice test of 10 min, the females who previously encountered a familiar demonstrator under cinnamaldehyde diet consumed a significantly higher proportion of cinnamaldehyde diet ($M_{\text{proportion}} = .71$, $SEM = .16$, 95% CI [0.40, 1.01], $n = 7$) than females previously confronted with a familiar demonstrator under eugenol diet ($M_{\text{proportion}} = .22$, $SEM = .12$, 95% CI [-0.03, 0.46], $n = 8$) ($p = .03$, $d = 1.10$, figure 1.2A). The same result was obtained during a choice test of 1 hr (cinnamaldehyde group: $M_{\text{proportion}} = .56$, $SEM = .14$, 95% CI [0.29, 0.82], $n = 7$; eugenol group: $M_{\text{proportion}} = .19$, $SEM = .08$, 95% CI [0.02, 0.35], $n = 8$) ($p = .04$, $d = 1.07$, figure 1.2B). This result suggests that the direct social transmission of food preference (STFP) between familiar female mice of wild origin was acquired.

Unfamiliar females

Social phase Unlike during the encounters between familiar females, the frequent occurrence of offensive agonistic behavior during encounters between

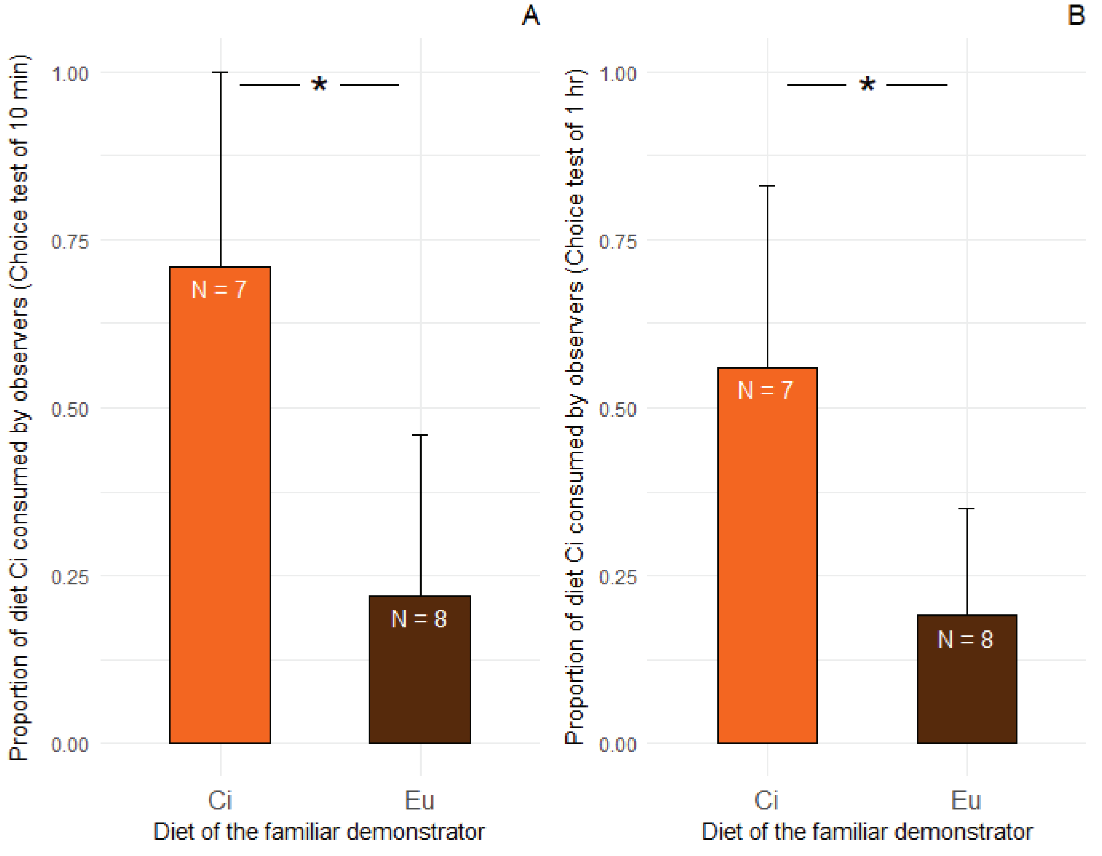

Figure 1.2 – Average proportion (M + 95% CI) of cinnamaldehyde diet consumed during a choice test of 10 min (A) and of 1 hr (B) by female observers in each experimental group after the encounter with a familiar female demonstrator. Ci: cinnamaldehyde; Eu: eugenol. Comparisons by Fisher Pitman permutation tests for independent samples ($*p < .050$).

unfamiliar females required the interruption of the experiment prior to the total duration of 900 s in ten of the 16 cases (M_{duration} = 371 s, *SEM* = 63, 95% *CI* [286, 456]). During the remaining six encounters, agonistic interactions between females did not occur (four in the cinnamaldehyde group and two in the eugenol group). The duration of investigation of the mouth area of demonstrators expressed by observers was significantly lower when offensive agonistic behavior was present during the encounter (M_{duration} = 20 s, *SEM* = 4, 95% *CI* [11, 28], $n = 10$) than when it was absent (M_{duration} = 46 s, *SEM* = 12, 95% *CI* [23, 69], $n = 6$) ($p = .03$, $d = 1.11$, figure 1.4A).

Choice test Three of the 16 tests were removed from the analysis of the choice test of 10 min because they did not meet the criteria necessary for the evaluation of the STFP (three observers did not consume any diet). The proportion of cinnamaldehyde diet consumed during the choice test of 10 min did not differ between the two experimental groups (cinnamaldehyde group: $M_{\text{proportion}} = .26$, *SEM* = .17, 95% *CI* [-0.08, 0.60], $n = 6$; eugenol group: $M_{\text{proportion}} = .31$, *SEM* = .16, 95% *CI* [0.00, 0.62], $n = 7$) ($p = .93$, figure 1.3A). During the choice test of 1 hr, females which previously encountered an unfamiliar female demonstrator under cinnamaldehyde diet ($M_{\text{proportion}} = .36$, *SEM* = .10, 95% *CI* [0.16, 0.55], $n = 8$) did not consume a significantly higher proportion of cinnamaldehyde diet than females previously encountering a demonstrator under eugenol diet ($M_{\text{proportion}} = .27$, *SEM* = .11, 95% *CI* [0.06, 0.48], $n = 8$) ($p = .57$, figure 1.3B).

Relation between behaviors expressed during the social phase and the acquisition of the STFP The diet preference index assessed during the choice test of 10 min did not differ significantly between cases when offensive agonistic behavior was present ($M_{\text{proportion}} = .49$, *SEM* = .16, 95% *CI* [0.20, 0.78], $n = 9$) or absent ($M_{\text{proportion}} = .50$, *SEM* = .29, 95% *CI* [-0.07, 1.07], $n = 4$) ($p = 1$). The same result was obtained during a choice test of 1 hr (group with presence of agonistic behavior: $M_{\text{proportion}} = .51$, *SEM* = .16, 95% *CI* [0.33, 0.69], $n = 10$; group with absence of agonistic behavior: $M_{\text{proportion}} = .60$, *SEM* = .18, 95% *CI* [0.25, 0.95], $n = 6$) ($p = 0.21$, figure 1.4B).

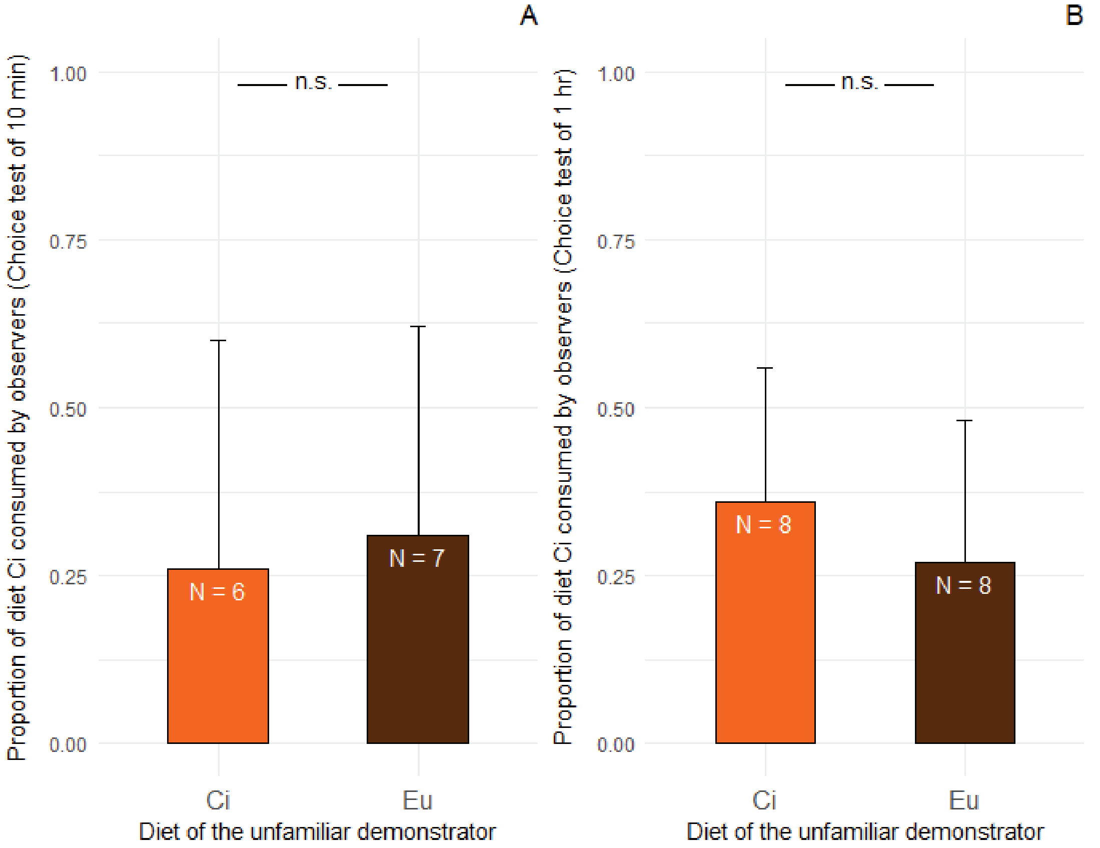

Figure 1.3 – Average proportion (M + 95% CI) of cinnamaldehyde diet consumed during a choice test of 10 min (A) and of 1 hr (B) by female observers in each experimental group after the encounter with an unfamiliar female demonstrator. Ci: cinnamaldehyde; Eu: eugenol. Comparisons by Fisher Pitman permutation tests for independent samples (n.s.: non-significant).

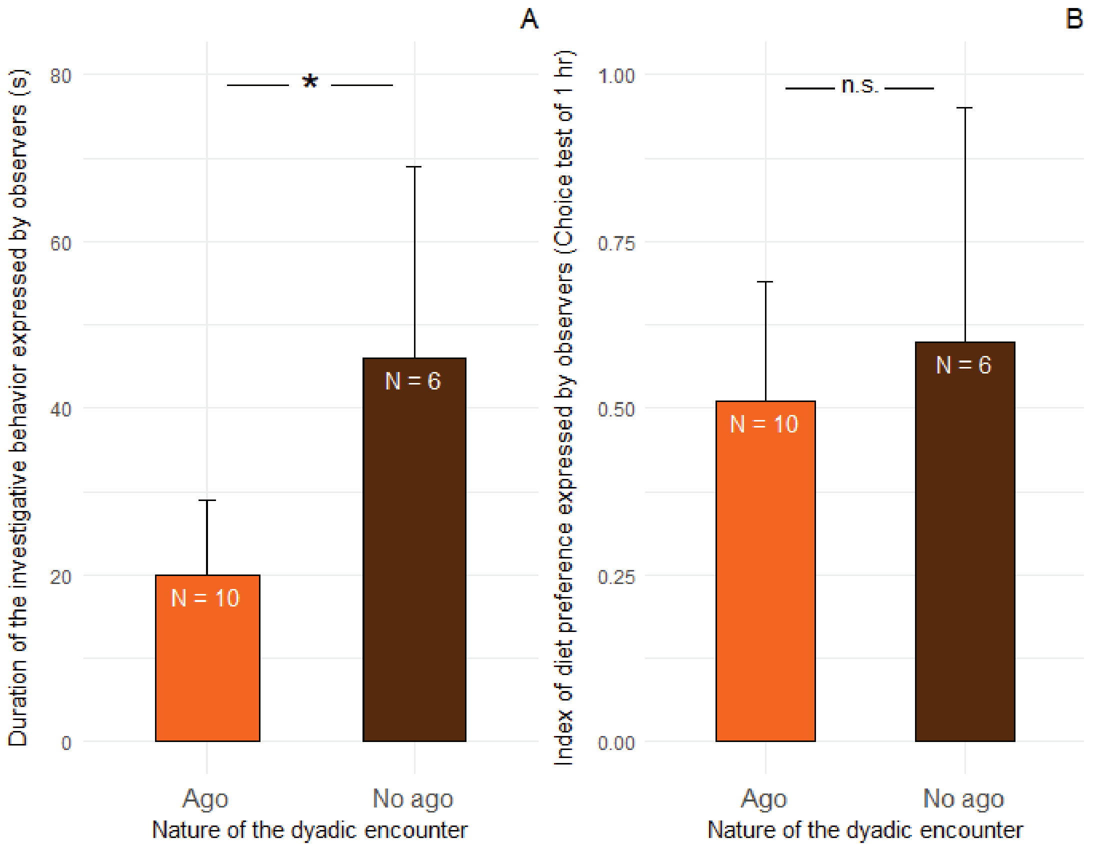

Figure 1.4 – Average duration (M + 95% CI) of investigative behavior expressed by female observers during the dyadic encounter (A) and average index of diet preference ($D/(D+O)$) (M + 95% CI) expressed by female observers, where D represents the quantity of the diet matching with the demonstrator's diet and O represents the quantity of the other diet consumed, during a choice test of 1 hr (B), depending on the presence (Ago) or absence (No ago) of offensive agonistic behavior. Comparisons by Fisher Pitman permutation tests for independent samples with stratification by the demonstrator's diet (*$p < .050$, n.s.: non-significant).

Experiment 2

Direct STFP between unfamiliar female house mice of wild origin

Fourteen of the 44 tests were removed from the analyses because they did not meet the criteria necessary for the evaluation of the STFP (four demonstrators did not consume the diet proposed during the consumption period and ten observers did not consume any diet during the choice test).

Social phase The frequent occurrence of offensive agonistic behavior during encounters between unfamiliar females required the interruption of the experiment prior to the total duration of 900 s in nine of the 30 cases ($M_{\text{duration}} = 327$ s, $SEM = 54$, 95% CI [220, 434]. Offensive agonistic interactions also occur in four additional encounters. During the remaining 17 encounters, agonistic interactions between females did not occur (10 in the oat group and 7 in the paste group). The duration of investigation of the mouth area of demonstrators expressed by observers was significantly lower when offensive behavior was present during the encounter ($M_{\text{duration}} = 30$ s, $SEM = 6$, 95% CI [18, 42], $n = 13$) than when it was absent ($M_{\text{duration}} = 45$ s, $SEM = 6$, 95% CI [34, 56], $n = 17$) ($p = .01$, $d = 0.63$, figure 1.6A).

Choice test During a choice test of 10 min, females having previously encountered a female demonstrator under oat diet ($M_{\text{proportion}} = .56$, $SEM = .12$, 95% CI [0.34, 0.79], $n = 15$) did not consume a significantly higher proportion of oat diet than females with a demonstrator under paste diet ($M_{\text{proportion}} = .47$, $SEM = .11$, 95% CI [0.26, 0.68], $n = 15$) ($p = .57$, figure 1.5A).

In addition, the speed of consumption of the oat diet did not differ significantly between the two experimental groups whatever the diet of the demonstrator (oat group: $M_{\text{speed of consumption}} = 5.15\ \text{mg}\,\text{s}^{-1}$, $SEM = 0.90$, 95% CI [3.00, 7.30], $n = 10$; paste group: $M_{\text{speed of consumption}} = 5.45\ \text{mg}\,\text{s}^{-1}$, $SEM = 1.54$, 95% CI [1.92, 8.98], $n = 11$) ($p = .91$, figure 1.5B). A similar result was obtained when we calculated the speed of consumption of the paste diet (oat group: $M_{\text{speed of consumption}} = 4.65\ \text{mg}\,\text{s}^{-1}$, $SEM = 0.69$, 95% CI [2.90, 6.39], $n = 9$; paste group: $M_{\text{speed of consumption}} = 4.24\ \text{mg}\,\text{s}^{-1}$, $SEM = 0.84$, 95% CI [2.22, 6.25],

$n = 10$) ($p = .77$).

Relation between behaviors expressed during the social phase and the acquisition of the STFP The index of diet preference assessed during the choice test of 10 min did not differ significantly between cases when agonistic behavior was present ($M_{\text{proportion}} = .67$, $SEM = .10$, 95% CI [0.47, 0.86], $n = 13$) or absent ($M_{\text{proportion}} = .45$, $SEM = .11$, 95% CI [0.23, 0.67], $n = 17$) during the encounter between unfamiliar females ($p = .17$, figure 1.6B).

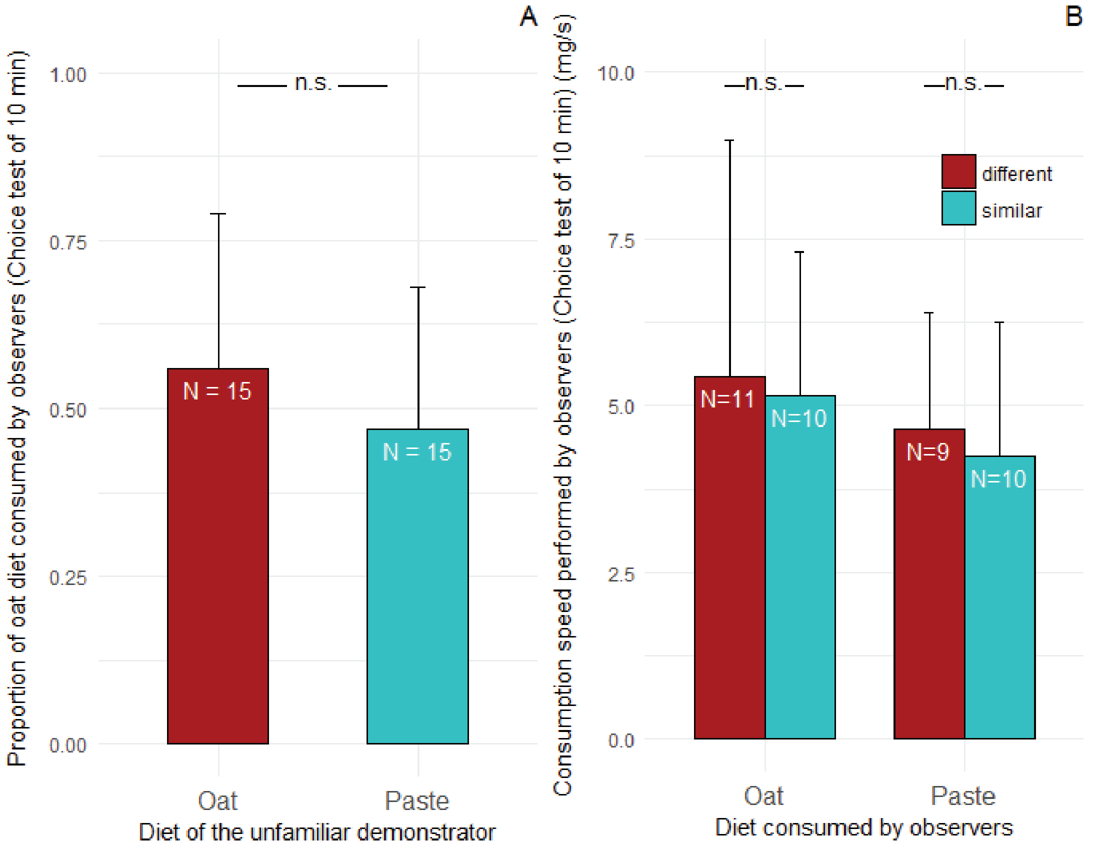

Figure 1.5 – Average proportion (M + 95% CI) of oat diet consumed by female observers in each experimental group (A) and comparisons of the average consumption speed (M + 95% CI) of each diet performed by the female observers according to the matching with the demonstrator's diet (B) after the encounter with an unfamiliar female demonstrator and during a choice test of 10 min. Comparisons by Fisher Pitman permutation tests for independent samples (n.s.: non-significant).

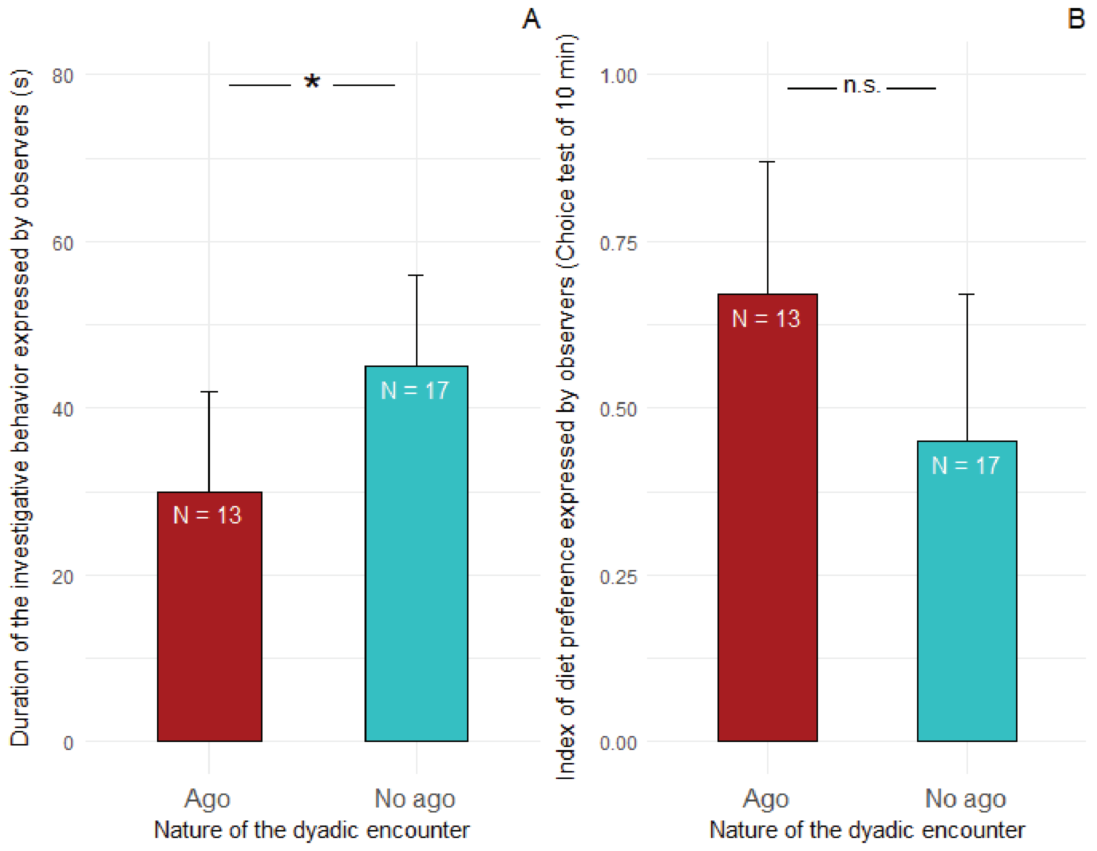

Figure 1.6 – Average duration (M + 95% CI) of investigative behavior expressed by female observers during the dyadic encounter (A) and average index of diet preference ($D/(D+O)$) (M + 95% CI) expressed by female observers, where D represents the quantity of the diet matching with the demonstrator's diet and O represents the quantity of the other diet consumed, during a choice test of 10 min (B), depending on the presence (Ago) or absence (No ago) of offensive agonistic behavior. Comparisons by Fisher Pitman permutation tests for independent samples with stratification by the demonstrator's diet ($^*p <$ .050, n.s.: non-significant).

Indirect STFP between unfamiliar female house mice of wild origin

Social phase Female observers spent on average 66% of their investigating time on the Petri dish carrying olfactory marks of their donor (oat group: $M_{\text{percentage}} = 70$ %, *SEM* = 2, 95% *CI* [66, 74], $n = 10$; paste group: $M_{\text{percentage}} = 61$ %, *SEM* = 4, 95% *CI* [53, 69], $n = 10$). They spent significantly more time on the dish carrying olfactory marks of a conspecific than on the control dish, regardless that their donor has consumed the oat diet (dish with olfactory marks: $M_{\text{duration}} = 34$ s, *SEM* = 4, 95% *CI* [27, 41]; control dish: $M_{\text{duration}} = 14$ s, *SEM* = 2, 95% *CI* [11, 18], $n = 10$) ($p = .002$, $d = 1.49$) or the paste diet (dish with olfactory marks: $M_{\text{duration}} = 28$ s, *SEM* = 5, 95% *CI* [18, 38]; control dish: $M_{\text{duration}} = 16$ s, *SEM* = 2, 95% *CI* [12, 20], $n = 10$) ($p = .02$, $d = 0.91$).

Choice test During a choice test of 10 min, female observers which previously have been exposed to olfactory marks of an unfamiliar donor under oat diet ($M_{\text{proportion}} = .48$, *SEM* = .09, 95% *CI* [0.29, 0.67], $n = 10$) consumed a significantly higher proportion of oat diet than females previously exposed to olfactory marks of a donor under paste diet ($M_{\text{proportion}} = .20$, *SEM* = .08, 95% *CI* [0.04, 0.36], $n = 10$) ($p = .04$, $d = 0.91$, figure 1.7A).

In addition, the speed of consumption of the oat diet was significantly higher in females with a donor under oat diet ($M_{\text{speed of consumption}} = 1.61\ \text{mg s}^{-1}$, *SEM* = 0.36, 95% *CI* [0.91, 2.32], $n = 10$) than for females with a donor under paste diet ($M_{\text{speed of consumption}} = 0.60\ \text{mg s}^{-1}$, *SEM* = 0.15, 95% *CI* [0.21, 0.99], $n = 6$) ($p = .049$, $d = 0.96$, figure 1.7B). A similar result was obtained for the speed of consumption of the paste diet, females with donors under paste diet consumed the paste diet faster ($M_{\text{speed of consumption}} = 5.19\ \text{mg s}^{-1}$, *SEM* = 0.91, 95% *CI* [3.41, 6.98], $n = 10$) than females with donors under oat diet ($M_{\text{speed of consumption}} = 2.77\ \text{mg s}^{-1}$, *SEM* = 0.39, 95% *CI* [1.92, 3.61], $n = 8$) ($p = .03$, $d = 0.95$). This result indicates that an indirect STFP between unfamiliar female mice of wild origin was acquired.

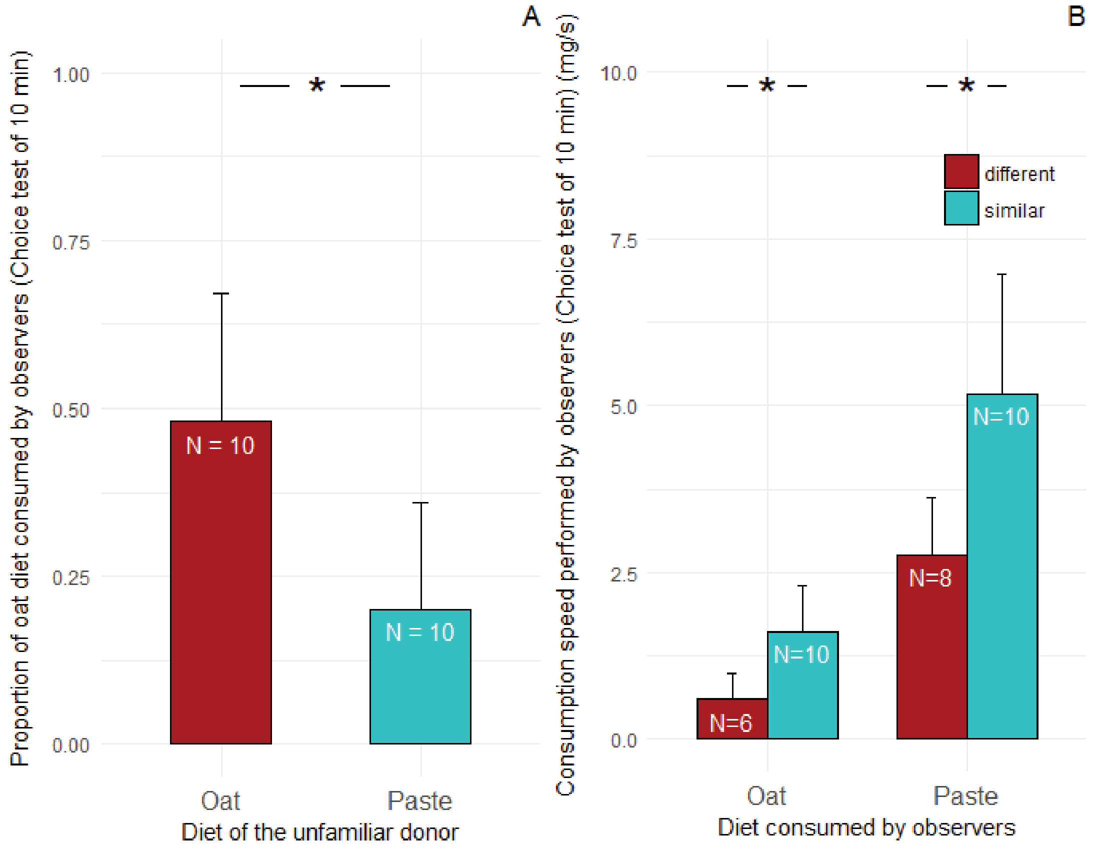

Figure 1.7 – Average proportion (M + 95% CI) of oat diet consumed by female observers in each experimental group (A) and comparisons of the average consumption speed (M + 95% CI) of each diet performed by the female observers according to the matching with the donor's diet (B) after the presentation of olfactory marks of an unfamiliar female donor and during a choice test of 10 min. Comparisons by Fisher Pitman permutation tests for independent samples ($^*p < .050$).

Relation between behaviors expressed during the social phase and the acquisition of the STFP The time the observer investigated the olfactory marks of the donor, which were applied to a Petri dish, was not significantly correlated with the observer's index of diet preference during the choice test of 10 min ($r = -0.18$, $p = .86$). That is, there were no indications for a relationship between the investigative behavior expressed by observers during the social phase and the acquisition of the indirect STFP.

Discussion

Our results suggest that direct social transmission of food preference (STFP) in female mice of wild origin is sensitive to familiarity. Using testing conditions similar to previous studies conducted with laboratory rodents (i.e. the use of diets of identical composition which differs by the addition of an odorant), a direct STFP was clearly established when the demonstrator was familiar but not when it was unfamiliar, regardless of the duration of the test (10 min or 1 hr). Using diets contrasting more in their constitutive elements does not improve direct STFP between unfamiliar individuals. However, STFP between unfamiliar females of wild origin was fully established when food information was captured indirectly, without a direct interaction between the unfamiliar females but from olfactory cues of a donor.

Whereas familiar female mice were able to acquire a direct STFP, house mouse females of wild origin did not achieve, under our testing conditions, a significant STFP when directly exposed to an unfamiliar demonstrator. Although our results do not refute a direct STFP, they unveil difficulties in establishing clear social learning under these testing conditions. Our results, obtained in house mice of wild origin, extend the findings reported in studies on Mongolian gerbils (Valsecchi et al., 1996) and domestic pigs (*Sus scrofa domesticus*) (Figueroa, Solà-Oriol, Manteca, & Pérez, 2013)) about the impairment of the direct STFP between unfamiliar and unrelated individuals. However, our results are not in agreement with those obtained in the study of Galef and Whiskin (2008), which have shown that not only direct STFP was effective between unfamiliar rats, but also that information from unfamiliar conspecifics can outweigh the relevance of information from familiar ones. This difference in findings could be explained by the high difference in social tolerance between wild and laboratory animals. Indeed, in our study, several encounters had to be interrupted because of repeated attacks between the demonstrator and the observer. Although less extreme than in males, intolerance between unfamiliar wild house mouse females is high (Hurst, 1987; Patris et al., 2002). This agonistic social context could affect STFP both by limiting the possibility of the animal to get in contact with the volatile compounds needed for information transmission and by altering the learning process (i.e., because of stress). Our results showed that the occurrence of offensive agonistic behavior during the encounter reduces the investigative behavior expressed by the observers. These results, differing from those obtained by Galef and Whiskin (2008) in laboratory rats whose investigative behavior was more sustained between unfamiliar individuals, reveal the differences between laboratory strains and wild strains. Our results, however, showed that although the duration of investigative behavior expressed by observers was altered by the presence of offensive agonistic behavior, this latter element did not appear to be related with the acquisition of the STFP. In our study, investigative behavior was present in all encounters. A short time of investigation being sufficient to induce the STFP (Galef & Stein, 1985), the opportunity for the observer to collect information for STFP was not called into question. The level of aggression observed during encounters may not be a sufficient condition to assess how stressful the context was for the observers. Indeed, although agonistic behavior is one of the major mechanisms by which social interactions result in an increase in stress hormone levels (Blanchard, McKittrick, & C., 2001; Ferrari, Palanza, Parmigiani, & Rodgers, 1998), another stress response pattern, characterized by immobility and low levels of aggression, can be observed in rodents (Koolhaas et al., 1999). Thus, even in absence of offensive agonistic behavior, the encounter, which induces a direct contact with an unfamiliar conspecific in a limited space, could be stressful enough to impair the acquisition of STFP.

Of course, other elements may play a role in STFP impairment and especially in females where there may be a hormonal effect. Previous studies have shown that the estrous cycle can affect the memory of STFP (Sanchez-Andrade et al., 2005). Because the phase of the estrous cycle of our female observers was not monitored during our experiments, it could be possible that the hormonal status of our females affected the acquisition of the STFP in one of the two situations, thus explaining the differences in learning. Nevertheless, additional studies have showed that, when tested immediately, STFP was in fact established whatever the cycle of the females but that the preference for the demonstrated diet lasted longer in diestrus and proestrus females than in estrus and ovariectomized mice (Choleris et al., 2011; Clipperton et al., 2008). In our experimental conditions, females were tested five min after the social phase and the duration of the choice test was short, so we can reasonably assume that the effect of estrogens on the learning abilities of our mice was reduced and was not sufficient to explain the absence of the direct STFP between unfamiliar females. Moreover, the replication of this procedure with diets of more contrasting nature in *Experiment 2* strongly suggests that the absence of STFP was due to the unfamiliarity of the demonstrator.

Several studies have shown that stress can affect learning and memory processes and in particular in the case of the STFP (Choleris et al., 2013). Indeed, the effects of stress on memory seem to follow an inverted U-shape where better learning performances occur in intermediate stressful conditions (Joëls, Pu, Wiegert, Oitzl, & Krugers, 2006; van der Kooij & Sandi, 2012). The level of stress during an encounter between unfamiliar females would then exceed the level facilitating the memorization process and preclude the establishment of the social learning process (Sandi & Pinelo-Nava, 2007). This suggestion was supported by the study of Choleris et al. (1998), which showed that the administration of the benzodiazepine mediated reduction of anxiety associated with the interactions between unfamiliar/unrelated gerbils, thus facilitating the acquisition of STFP. Under stressful circumstances, anxiety can increase attention to threat-related stimuli present in the environment and can affect cognitive performance that requires taking into account other stimuli (Eysenck, Derakshan, Santos, & Calvo, 2007). In these conditions, the presence of a potentially aggressive conspecific may be sufficient to alter the perception and the use of diet information by the observer.

The present study showed that with olfactory marks, indirect STFP was effective between unfamiliar females. During the choice test, the speed of consumption of a diet increased with the perception of this diet in olfactory marks of the donor. These results were validated for both diets and suggest that mice became more confident about the quality of a new food item when they had experienced it through the olfactory marks of a conspecific. These results were robust although the observers of both groups consumed consistently more paste diet than oat diet. The two diets differed in their composition and the caloric value is clearly higher in the paste diet. This stronger attraction for paste diet, despite the effective STFP, highlights that elements related to the quality of food such as palatability and caloric content are taken into account by individuals when they select a new food item. A study in the meadow voles showed that the protein content of the diet can influence the attractiveness of olfactory marks of a conspecific and the authors suggested that the odor change could be due to "an increase of the concentration of proteins, amino acids or other metabolic products" (Ferkin et al., 1997). In our case, even if we do not know what chemical changes occurred in the olfactory marks of a conspecific under a certain diet, the information perceived by mice in olfactory marks were sufficient to allow them to make the connection with the diet itself. This suggests that some of the odorant compounds related to the diet are present in the olfactory marks of mice after the diet consumption.

Our results showing indirect communication, obtained in house mice of wild origin, extend the findings reported in studies on laboratory rats (Laland & Plotkin, 1991) and laboratory mice (Arakawa et al., 2013). Mice and rats are capable of independently perceiving information about diet and individual identity in the body odors of conspecifics (Brown, Schellinck, & West, 1996; Colombelli-Négrel & Gouat, 2006; Kwak et al., 2008). Although the mice in our experiment could detect that donors were unfamiliar individuals, STFP was clearly effective. The efficiency of indirect STFP between unfamiliar females supports our hypotheses explaining the difficulties in achieving direct STFP between unfamiliar females. Indeed, by this result, we show that the impairment of direct STFP was not a consequence of the origin of social information (i.e. an unfamiliar mouse and a potential competitor), leading us to suspect that this impairment was related to the stressful situation regarding the presence of a potential competitor (i.e. the demonstrator).

In conclusion, the results of the present experiments demonstrate that in house mice of wild origin, familiarity can affect the acquisition of social information during a social interaction. In addition, the clear establishment of indirect STFP between unfamiliar females suggests that the necessary conditions allowing acquisition of STFP seems more related to the social context in which the individual can acquire information than to the familiarity of the conspecific. Thus, we showed that social context can modulate the acquisition of STFP. Relying on olfactory marks of conspecifics appears to be less costly regarding social constraints, and therefore these marks can be considered as sources of reliable information by mice, which would then widen the range of potential feeding items in natural conditions. Moreover, they can share this new knowledge with their social groups by direct STFP.

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Chapter 2

Necessary conditions for social transmission of food preference through feces in the house mouse

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Necessary conditions for social transmission of food preference through feces in the house mouse, *Mus musculus domesticus*

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Acknowledgments

We gratefully thank Fabrice Savarit for chemical advices.

Submitted for publication in *Chemical Senses*.

Abstract

Mice can obtain information about a new food source through olfactory cues of conspecifics and consequently develop an attraction for this diet. The social transmission of food preference (STFP) takes place directly, during an encounter with a conspecific or indirectly, via feces. In indirect STFP, the digestive process can degrade odorant compounds characterizing the food, impairing the matching between feces and food. In a previous study, indirect STFP was efficient when the information support was a composite odorant. We, thus, hypothesized that the acquisition of indirect STFP depends on the multiplicity of the odorant molecules present in diets. Tested in female house mice (*Mus musculus domesticus*) our results showed that, single odorant molecule as information support was not sufficient to induce an indirect STFP. Chemical analysis did not reveal the presence of the molecules in feces suggesting that the degradation of diet cues during the digestive process prevented the pairing between feces and food. By using a process which limits the degradation of molecules, we performed indirect STFP when the pertinent information was represented by single odorant molecule and multiple odorant molecules. Unlike with multiple odorant molecules, our results did not show a clear indirect STFP with single odorant molecule, despite their presence in feces confirmed by chemical analysis. We conclude that constraints associated to indirect STFP can be removed by the multiplicity of information characterizing the diet both by reducing the degradation risk during the digestive process and by allowing an accurate assessment of diet consumed by the conspecific.

Keywords: choice test, digestive process, odorant molecules, olfactory perception, rodents.

Introduction

For most species of rodents, olfaction is an important source of information to assess their environment including the social one. Rodents depend on the emission and detection of olfactory cues for social recognition and social learning and have developed high sensitivity in discriminating and memorizing the chemo-signals perceived from conspecifics (Sanchez-Andrade & Kendrick, 2009; Brennan & Keverne, 2015). For instance, rodents are able to use olfactory information on novel food sources from experienced conspecifics in order to enlarge their food repertoire (Galef & Wigmore, 1983; Posadas-Andrews & Roper, 1983; Strupp & Levitsky, 1984; Valsecchi & Galef, 1989).

Under laboratory conditions, the social transmission of food preference (STFP) is possible during an encounter with a conspecific demonstrator (referred to as "direct STFP" hereafter) thanks to the formation of an association between a natural constituent present in the rodent's breath, the carbon disulfide (CS_2) and the odor of the consumed diet (Galef, Mason, Preti, & Bean, 1988). Then, the acquired information may be expressed by the tested individual (called the observer) in a choice situation between 2 new food items, one of which is the kind of food consumed by the demonstrator. A crucial step allowing the STFP results, therefore, in the flexible expression of a relational memory (Alvarez, Lipton, Melrose, & Eichenbaum, 2001) and in the matching between the diet odor perceived from the conspecific and the odor of the diet itself during the choice test.

During the direct STFP, the odor of the new diet comes from the breath and the food scraps present on the demonstrator's mouth area. Thus, the food odor perceived from the demonstrator should not differ from the odor of the food itself. In studies in mice, direct STFP was established when the information characterizing the diet was carried by composite odorants (Valsecchi & Galef, 1989) and single odorant molecule (Forestier, Féron, & Gouat, In-Press), suggesting a complete conservation of diet information during direct STFP.

More recently, it has been shown that the guanylyl cyclase receptor, the specific receptor responding to carbon disulfide, also responds to uroguanylin, a peptide present in the urine and feces of rodents (Munger et al., 2010). This peptide acts as a social stimulus in the same way as carbon disulfide and promotes the STFP in mice via the feces of a donor conspecific (referred to as "indirect STFP" hereafter) (Arakawa et al., 2013). This second way of STFP offers the advantage, at least in laboratory experiments, of reducing the constraints associated with the presence of a conspecific, particularly in the case of social intolerance between individuals (Forestier et al., In-Press). However, contrary to direct STFP, the indirect STFP implies a transformation of food characteristics by the digestive system which could alter the original information related to the diet. In this case, some olfactory compounds may not be found in the donor's feces making the matching between diet odor perceived from the feces of the conspecific and the odor of the diet itself difficult. In the study of Arakawa et al. (2013), donor mice were fed with powdered chow adulterated with either cocoa or cinnamon powder (food additives). As a consequence, for each diet, the information support comprises a large number of different odorant molecules. Under these conditions indirect STFP revealed to be efficient. We, thus, hypothesized that the acquisition of indirect STFP depends on the multiplicity of the odorant molecules present inside the diet. Because the absorption or degradation of molecules during the digestive process depends in part on their molecular structure (Drożdż, 1968; Choonara et al., 2014), we expected that in the diversity of elements characterizing the food, some odorant characteristics of the food will be preserved and that they should be sufficient for mice to match the odor from the feces with the food during the choice test.

To test our hypothesis, we assessed the efficiency of foods differing in their capacity to be a good support for indirect STFP in house mice (*Mus musculus domesticus*). As described in the study of Arakawa et al. (2013), we used diets of the same composition differing by the addition of different odorants. The odorant molecules used were specifically selected because they were easily detectable by gas-chromatography coupled with mass-spectrometry (GC-MS) through headspace analysis by Solid Phase Micro-Extraction (SPME). This allowed us to assess both their presence in diets and their presence in donor's feces.

The acquisition of indirect STFP was firstly tested when the information allowing the identification of the diet was reduced to a single odorant molecule. Under these conditions, we expected a degradation of food information during the digestive process that would affect the establishment of indirect STFP.

In order to improve the availability of food information in the feces, we then tested the effectiveness of the indirect STFP when the food was characterized by a single odorant molecule which was protected from the digestive process. The use of this protection should preserve the characteristic odorant molecule inside donor's feces and allow the acquisition of the indirect STFP.

Finally, to ensure that the protection was not an element that could affect the acquisition of the STFP, we mimicked the experimental conditions used by Arakawa et al. (2013) by testing the acquisition of the indirect STFP when the information allowing the identification of the diet was represented by multiple odorant molecules. Under these conditions, we would also expect STFP to take place.

Material and methods

Animals and breeding conditions

The animals used in this study were house mice, *Mus musculus domesticus*, descendants from animals of wild origin provided and bred for more than 10 generations by the laboratory RS2GP of VetAgro Sup Lyon (France). The mice were bred in our laboratory for 7 generations with addition of wild animals captured at different sites in France, in the Die region (Vachères en Quint 44.789720 N, 5.259654 E, Montlaur en Diois 44.789720 N, 5.259654 E) and in the Beaujolais region (Chambost-Allières 46.012944 N, 4.481324 E).

We used 120 adult females ($M_{age} \pm SEM$: 164 ± 3 d) from 25 breeding pairs in the present study.

Mice were housed in standard cages (365 × 207 × 140 mm) with a bedding of wood shavings (Special Diet Services, Witham, Essex, U.K.) and cotton as nesting material. All mice received water and pelleted food (type M20, Special Diet Services, Witham, Essex, U.K.) *ad libitum*. The room in which the mice resided was environmentally controlled on a 14:10-h-light-dark cycle (19:00-9:00-h lighting) at a temperature of 20 ± 2 °C and relative humidity of 50-60%. During the dark phase, the room was lit by a red light (2 neon tubes, 35 W) allowing observation by the experimenter. The mice were weaned at 21 days of age and were placed in same-sex sibling groups 1 week later. At least 1 week before the experiment, animals were transferred to the experimental room. Females were placed by pairs of sisters in new cages but were tested individually. Mice were individually marked by hair clipping when necessary.

Diets

Diets used in these experiments derived from baits originally designed to control rodent pest populations. The bait used was an artificial paste with high lipid content. The diets were specifically manufactured for these experiments by Liphatech (Liphatech S.A., Pont du Casse, Lot et Garonne, France) and did not contain any rodenticide. In each experiment, we used 2 diets of the same composition that differed by the addition of specific odorants.

In *Experiment 1*, the 2 diets differed by the addition of a single odorant molecule: either 0.1% of cinnamaldehyde (referred to as "cinnamaldehyde diet" hereafter) or 0.1% of eugenol (referred to as "eugenol diet" hereafter).

In *Experiment 2*, a protective envelope (referred to as "protected diet" hereafter), specifically manufactured for this study by Liphatech and AB7 Innovation (AB7 Innovation, Deyme, Haute-Garonne, France) and whose constitution cannot be revealed because of confidentiality, was used in each diet. The 2 diets differed by the addition of a single odorant molecule: either geraniol (referred to as "Protected-geraniol diet" hereafter) or eugenol (referred to as "Protected-eugenol diet" hereafter). For both diets, each single odorant molecule associated with the protective envelope represented 2.5% of the diet composition.

In *Experiment 3*, the 2 diets differed by the addition of multiple odorant molecules. In order to create blends of multiple odorant molecules corresponding to natural odorants, we used the major compounds found in Damascus rose essential oil (35% geraniol, 35% nerol, 10% 2 phenyl-ethyl alcohol, 5% geranyl acetate and 15% nonadecane) (Babu, Singh, Joshi, & Singh, 2002) and clove essential oil (85% eugenol, 5% β-caryophylene and 10% eugenyl acetate) (Alma, Ertas, Nitz, & Kollmannsberger, 2007) (respectively referred to as "Protected-Damascus rose diet" and "Protected-clove diet" hereafter). For both diets, all odorant compounds associated with the protective envelope (see details above) represented 2.5% of the diet composition.

Procedure for chemical analyses

Method

For headspace sampling, SPME was performed with a fiber of a 65 µm Polydimethylsiloxane/ Divinylbenzene (Supelco), which was inserted into the glass vial containing the sample for 10 min and then immediately injected into the GC-MS. We used an Agilent 6890N gas-chromatograph (capillary column: Agilent HP-5MS, 30 m × 25 µm × 0.25 µm; split-splitless injector at 250 °C; carrying helium gas at 1 mL/min) coupled to an Agilent 5975C mass spectrometer, with 70 eV electron impact ionization. Fiber desorption lasted 5 min and the oven temperature program was: from 40 °C to 100 °C at 10 °C/min, and then to 280 °C at 5 °C/min, hold for 5 min.

Sample analysis

In order to identify the odorant molecules, 200 µL of each compound (exept eugenyl acetate and nonadecane) were placed in a glass vial of 2 mL and firstly analyzed with the SPME fiber. A solution in pentane (HPLC grade from Sigma Aldrich) has been prepared for eugenyl acetate and nonadecane (0.4 g/L). Eugenol and cinnamaldehyde were obtained from Sigma Chemical Company (Sigma-Aldrich S.a.r.l., Saint Quentin Fallavier, Isère, France) and the remaining compounds (geraniol, nerol, 2 phenyl-ethyl alcohol, geranyl acetate, nonadecane, β-caryophylene and eugenyl acetate) were provided by Liphatech.

The detection of the molecules by the GC-MS when they are contained in the paste diet were then verified by analyzing samples of each odorant diet (cinnamaldehyde diet, eugenol diet, Protected-eugenol diet, Protected-geraniol diet, Protected-Damascus rose diet, Protected-clove diet) (0.25 g).

Finally, to assess the impact of the digestive process on the molecules conservation, an analysis of the feces of mice that had consumed one of the odorant diets were performed. To obtain a sufficient quantity of feces for chemical analy-

	Donors	**Donor's diet**	**Donor's consumption** mean ± standard error (g)
Exp.1	$N = 8$	Cinnamaldehyde diet	8.78 ± 0.15
		Eugenol diet	8.96 ± 0.04
Exp.2	$N = 8$	Prot-geraniol diet	5.94 ± 0.71
		Prot-eugenol diet	8.61 ± 0.27
Exp.3		Prot-Damascus rose diet	7.06 ± 0.87
		Prot-clove diet	8.46 ± 0.54

Table 2.1 – Number of female mice donors used for chemical analyses and average consumption of the 9 g of experimental diet offered after 72 hr of feeding period. Prot-: diet with a protective envelope.

ses, donors were given 9 g per individual of an experimental diet simultaneously with the standard diet during 72 hr. The consumption of the diet was verified at the end of this period (table 2.1). The artificial paste was colored and therefore the feces were colored. This color indicator was used to collect feces that were excreted after diet consumption and feces of each donor (0.25 g) were placed in a glass vial. Each glass vial was then placed in a sealed freezer bag at −20 °C until required.

16 female mice, different from those used for behavioral experiments, were used as donors; 8 individuals served as donors for the diets without protection and 8 additional individuals served as donors for the protected diets. The presentation order of each diet was randomly assigned and balanced and a delay of 1 week was respected before placing donors under another odorized diet.

For each analysis, the compounds were identified on the basis of their mass spectra and retention times by comparing them to the mass spectral library NIST 2008 and with standards.

Procedure for behavioral experiments

The general paradigm used in this study was based on the different procedures developed to test the social transmission of food preference (STFP) in rats and mice where each experiment encompassed a social phase followed by a choice test (Arakawa et al., 2013; Galef & Wigmore, 1983; Posadas-Andrews &

Roper, 1983; Valsecchi & Galef, 1989). During the social phase, a naïve observer mouse was confronted with social information about a given diet through the presentation of feces of a conspecific donor. Each experiment included 2 groups of animals differing in the nature of the diet experienced by the donor. During the choice test, the observer was confronted with the 2 diets. The STFP was considered as being acquired when the 2 groups differed significantly in their food consumption.

Social phase

Donors were placed in clean individual standard polycarbonate cages with a bedding of wood shavings and cotton as nesting material. They were given 3 g per day of 1 of the 2 diets simultaneously with the standard diet during 24 hr (Experiment 1). Because donors were less likely to consume the other diets at 24 hr (part of the donors in each group consumed less than 50% of the diet), the duration of the feeding period was extended to 72 hr in the following experiments to increase their diet consumption (*Experiment 2* and *Experiment 3*). The consumption of the diet was quantified at the end of the feeding period (table 2.2).

The feces of donors were collected during the lit period (0.10 – 0.20 g per sample). The color indicator was used to collect feces that were excreted after diet consumption. Each sample was placed in a sealed freezer bag and placed at −20 °C until required. On the day of the experiment, the feces sample was thawed 30 min before the beginning of the social phase. Feces were placed in a clean Petri dish (35 mm in diameter) fixed on a plexiglas support together with another clean Petri dish (control) to verify that the observer perceived the odorant stimulus (Colombelli-Négrel & Gouat, 2006), each separated by a vertical wall (75 mm high). The position of each dish on the support (left/right) was randomly assigned and balanced across trials. The social phase occurred during the dark period. The observer was placed in a clean cage and had 5 min to acclimate to the cage. A transparent tray was placed on the cage to prevent observers from escaping, and to allow observation. The support with the dishes was introduced into the cage. The presentation of the feces lasted 10

	Observers	Donors	Donor's diet	Donor's consumption mean ± standard error (g)
Exp.1	$N = 16$	$N = 8$	Cinnamaldehyde diet	2.95 ± 0.05
		$N = 8$	Eugenol diet	2.99 ± 0.01
Exp.2	$N = 20$	$N = 9$	Prot-geraniol diet	1.63 ± 0.23
		$N = 10$	Prot-eugenol diet	2.47 ± 0.11
Exp.3	$N = 20$	$N = 8$	Prot-Damascus rose diet	2.31 ± 0.20
		$N = 5$	Prot-clove diet	2.67 ± 0.33

Table 2.2 – Number of female mice used in each behavioral experiment and average consumption of donors of the 3 g of experimental diet offered after 24 hr of feeding period (*Experiment 1*) and average consumption per 24 hr of the 9 g of experimental diet offered after 72 hr of feeding period (*Experiment 2* and *Experiment 3*). Prot-: diet with a protective envelope.

min starting with the first contact of the mouse with the support. Investigation time of each dish was measured from a video-recording of the experiment (Sony FDR-AX100E). At the end of the social phase, the support was removed and the observer was transferred to a clean test cage. The choice test (see below) began 5 min later. Donors were all unfamiliar and unrelated with their respective observers (table 2.2).

Choice test

For each experiment, the procedure of choice test was the same. A 3 g sample of each diet was placed in a Petri dish to limit the dispersion of unconsumed food. The 2 Petri dishes were fixed to a support of the same type as the one described in the social phase and then placed inside the test cage. The position (left/right) of each diet was randomly assigned and balanced across trials. The support with the diets was introduced into the test cage and the test began from the first contact of the mouse with the support. At the end of the test, the observer was returned to its home cage. The remaining food was carefully collected inside the cage and the amount of unconsumed food was weighed to the nearest 0.02 g using a digital balance.

In *Experiment 1*, the duration of the choice test (1 hr) was the same as that used in the study highlighting the indirect STFP (Arakawa et al., 2013). During the test, observers did not have access to standard diet and water.

In *Experiment 2* and *Experiment 3*, to improve the diet consumption of observers, we extended the test to 24 hr. This duration corresponded to the usual duration of previous studies on direct STFP (Galef & Whiskin, 2008; Valsecchi & Galef, 1989). At 1 hr of the test, observers received water and standard diet ad libitum and cotton as nesting material.

Behavioral data analysis

The data collection and analysis were done blind to group identity to remove any source of unintentional bias. Because of the small number of animals in each group ($N < 15$), we used non parametric statistics. The results were significant when $p \leq 0.050$ and the data were reported by their mean (M) and standard error (SEM). We also reported the effect size by using the Cohen's d value. All statistical comparisons were performed with the software StatXact (Cytel Software Corporation, 2010).

For each experiment, we verified that observers perceived the odorant stimulus during the social phase by comparing their duration of investigative behavior for each dish present on the device (feces vs. control). Fisher Pitman permutation tests for paired samples were used for these comparisons.

In *Experiment 1*, the acquisition of the STFP was assessed by comparing the proportion of cinnamaldehyde diet consumed by the observers of the 2 experimental groups (cinnamaldehyde group vs. eugenol group) during the choice test (Galef & Wigmore, 1983). The proportion of cinnamaldehyde diet corresponded to the ratio of the quantity of cinnamaldehyde diet consumed over the total consumption (total quantity consumed) of both diets.

In *Experiment 2*, we evaluated the establishment of the STFP by comparing the proportion of Protected-geraniol diet consumed by the observers of the 2 experimental groups (Protected-geraniol group vs. Protected-eugenol group) during the choice test.

In *Experiment 3*, the acquisition of the STFP was assessed by comparing the proportion of Protected-Damascus rose diet consumed by the observers of the 2 experimental groups (Protected-Damascus rose group vs. Protected-clove group) during the choice test.

To evaluate the establishment of the indirect STFP, we used Fisher Pitman permutation tests for independent samples.

Ethics note

Experimental procedures were approved by the French ethics committee "Charles Darwin C2EA 05" (reference number 04355.02). This study did not require euthanasia of mice at the end of experiments and subjects were therefore retained for later use.

Results

Experiment 1

Social phase

Female observers spent significantly more time on the dish with feces of a conspecific donor than on the control dish, regardless that their donor has consumed the cinnamaldehyde diet ($M_{duration} \pm SEM$; dish with feces: 58 ± 7 s, control dish: 34 ± 10 s, $n = 7$) ($p = 0.047$, Cohen's $d = 0.97$) or the eugenol diet ($M_{duration} \pm SEM$; dish with feces: 53 ± 5 s, control dish: 34 ± 5 s, $n = 8$) ($p = 0.04$, Cohen's $d = 1.14$) (figure 2.1A).

Choice test

During the choice test of 1 hr, female observers which have been previously exposed to feces of an unfamiliar female donor under cinnamaldehyde diet did not consume a significantly higher proportion of cinnamaldehyde diet than females previously exposed to feces of a donor under eugenol diet ($M_{proportion} \pm SEM$; cinnamaldehyde group: 0.25 ± 0.12, $n = 8$, eugenol group: 0.11 ± 0.05, $n = 8$) ($p = 0.31$, Cohen's $d = 0.56$) (figure 2.1B).

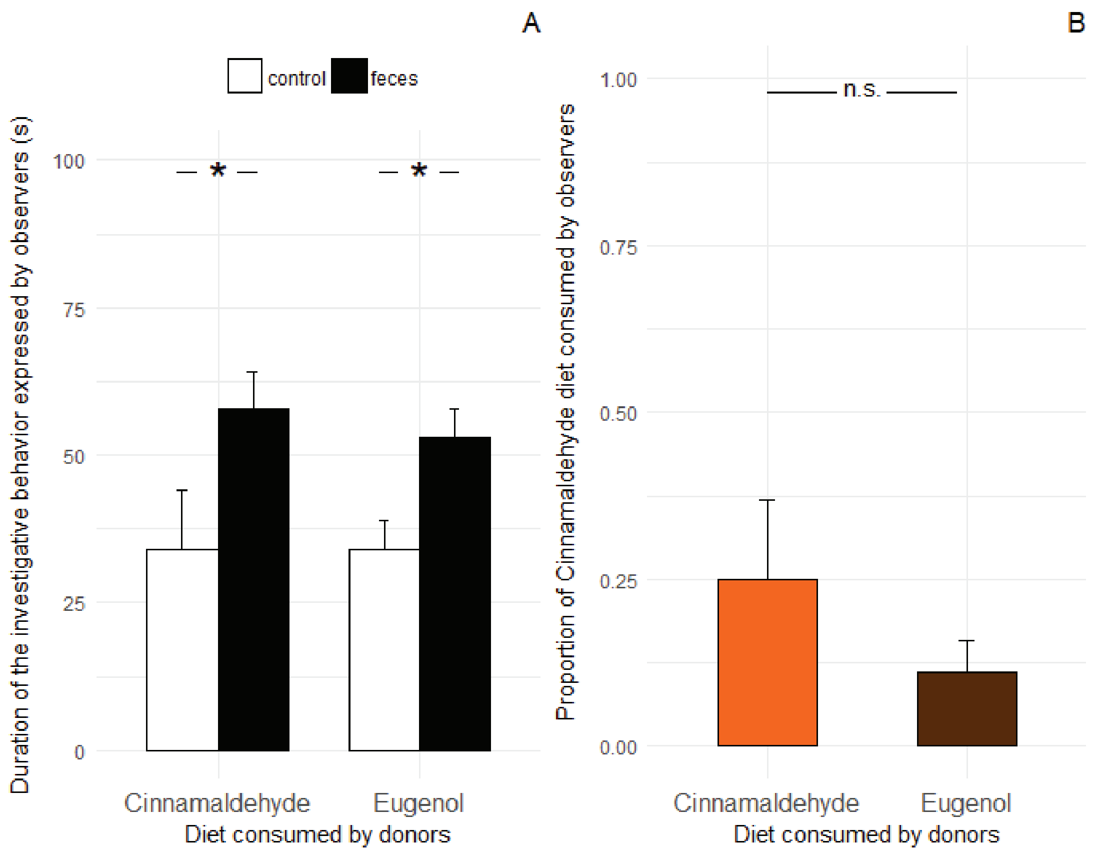

Figure 2.1 – Average duration ($M + SEM$) of investigative behavior on each dish presented during the social phase (A) and average proportion ($M + SEM$) of cinnamaldehyde diet consumed and during a choice test of 1 hr (B), expressed by female observers in each experimental group ($n = 8$ in each group). Comparisons by Fisher Pitman permutation tests for paired samples (A) and independent samples (B) ($^*p < 0.050$, n.s.: non-significant).

Chemical analyses

The analysis of synthetic standards revealed that both cinnamaldehyde (annex 2.6A) and eugenol (annex 2.7A) could be clearly detected by the GC-MS under our experimental conditions.

The analysis of the artificial paste representing the diets revealed the presence of the cinnamaldehyde peak in the cinnamaldehyde diet (annex 2.6B) and of the eugenol peak in the eugenol diet (annex 2.7B), showing that these molecules could be easily detected by head-space analysis under our experimental conditions.

However, the chemical analyses of the feces of the female donors having consumed either the cinnamaldehyde diet ($n = 8$) or the eugenol diet ($n = 8$) did not reveal the presence of cinnamaldehyde or of eugenol in the samples.

Experiment 2

Chemical analyses

Under our experimental conditions, the synthetic geraniol could be clearly detected (annex 2.8).

In the same way, geraniol could be detected in samples containing the Protected-geraniol diet (figure 2.2A), and eugenol could be detected from samples from the Protected-eugenol diet presented (figure 2.2C).

In addition, chemical analyses revealed the presence of geraniol in the feces samples of all female donors having consumed the Protected-geraniol diet ($n = 8$, figure 2.2B). A similar result was obtained for eugenol in all feces samples of the female donors under Protected-eugenol diet ($n = 8$, figure 2.2D).

Social phase

Female observers spent significantly more time on the Petri dish carrying feces of a conspecific donor than on the control dish, regardless whether their donor has consumed the Protected-geraniol diet ($M_{duration} \pm SEM$; dish with feces: 51 ± 7 s, control dish: 21 ± 3 s, $n = 10$) ($p = 0.01$, Cohen's $d = 1.36$) or the

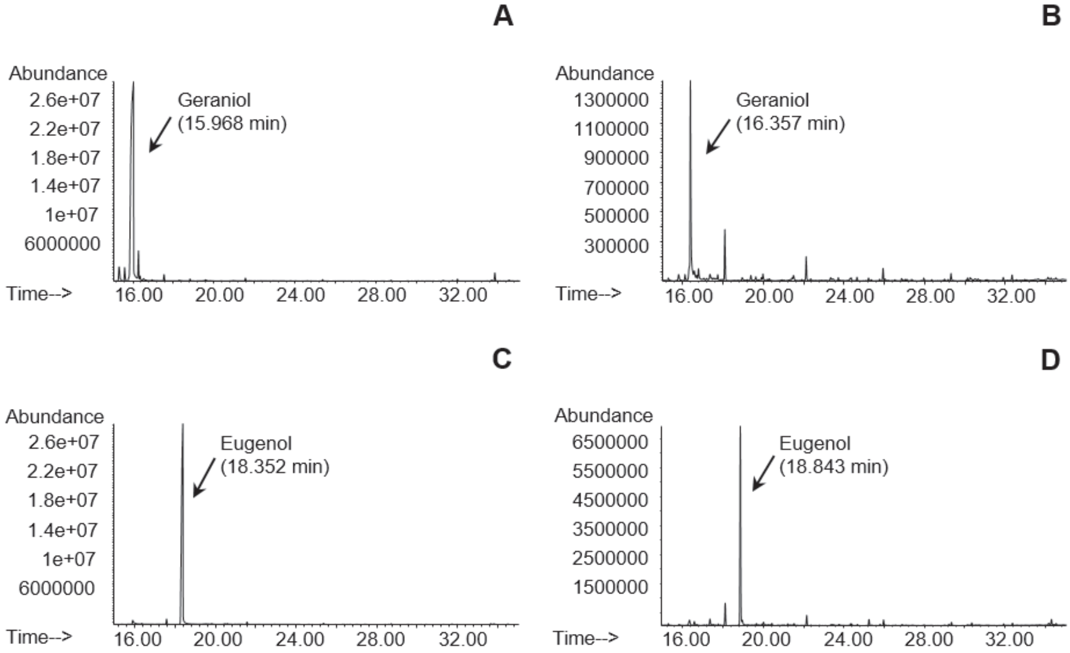

Figure 2.2 – Gas-chromatograms showing the detection of geraniol in a Protected-geraniol diet samples (A) and in the feces of a female donor under the Protected-geraniol diet (B); and the detection of eugenol in a Protected-eugenol diet sample (C) and in the feces of a female donor under the Protected-eugenol diet (D).

Protected-eugenol diet ($M_{duration} \pm SEM$; dish with feces: 77 ± 10 s, control dish: 32 ± 4 s, $n = 10$) ($p = 0.01$, Cohen's $d = 1.35$) (figure 2.3A).

Choice test

During the choice test of 24 hr, female observers having previously investigated feces of a female donor under Protected-geraniol diet did not consume a significantly higher proportion of Protected-geraniol diet than females with a donor under Protected-eugenol diet ($M_{proportion} \pm SEM$; Protected-geraniol group: 0.44 ± 0.07, $n = 10$, Protected-eugenol group: 0.34 ± 0.08, $n = 10$) ($p = 0.36$, Cohen's $d = 0.42$) (figure 2.3B).

Experiment 3

Chemical analyses

Chemical analyses of synthetic standards revealed that each odorant molecule present in Protected-Damascus rose diet (geraniol, nerol, 2 phenylethyl alcohol, geranyl acetate and nonadecane) (annex 2.9) and in Protected-clove diet (eugenol, β-caryophyllene and eugenyl acetate) (annex 2.10) could be detected by GC-MS under our experimental conditions.

Similarly, chemical analysis of samples of the Protected-Damascus rose diet revealed the presence of all odorant molecules characteristic of this diet (figure 2.4A). A similar result was observed for the molecules characteristic of the Protected-clove diet (figure 2.4C).

However, whatever the diet consumed by the donor, not all the odorant molecules included originally in the diet were detected in the corresponding feces profiles. All feces profiles of donors under Protected-Damascus rose diet (n= 8, figure 2.4B) revealed the presence of geraniol and nerol, but nonadecane and geranyl acetate were found in 6 of the 8 profiles. None of the feces samples, revealed the presence of 2-phenylethyl alcohol. Eugenol and β-caryophyllene were detected in all profiles of donors under Protected-clove diet ($n = 8$, figure 2.4D), but only 1 profile revealed the presence of eugenyl acetate.

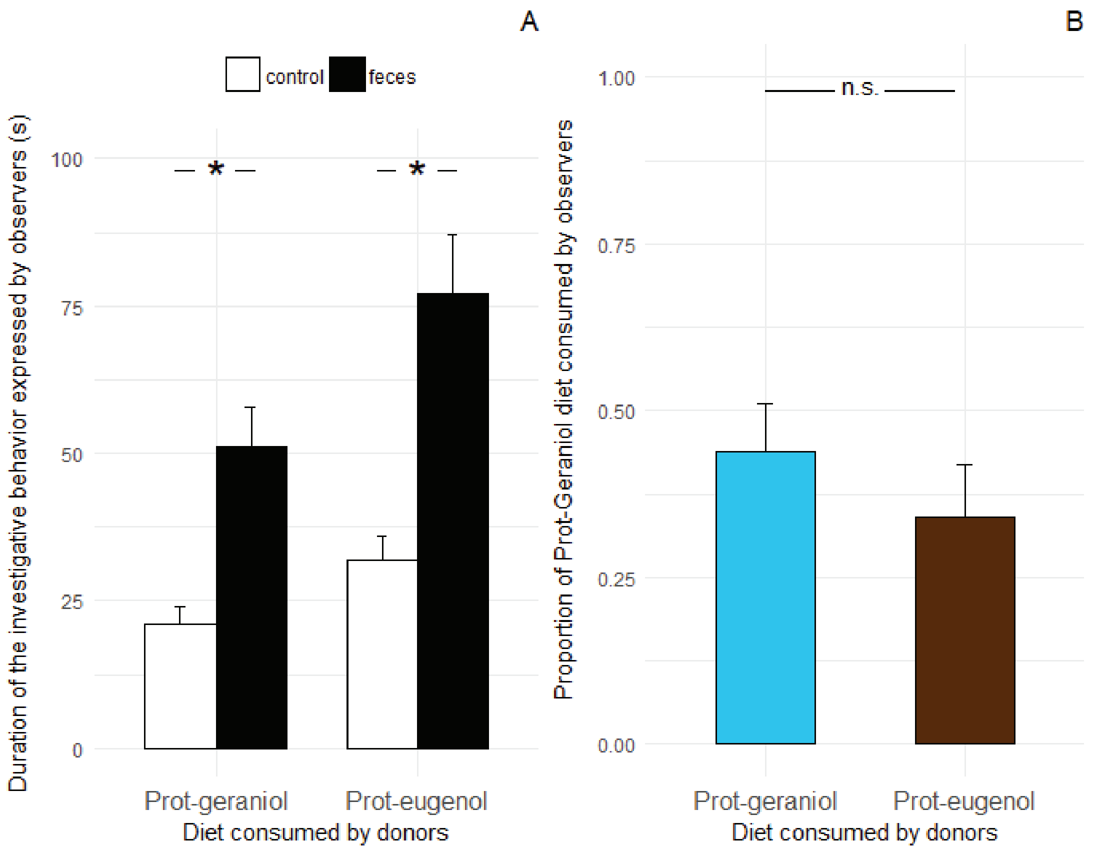

Figure 2.3 – Average duration ($M + SEM$) of investigative behavior on each dish presented during the social phase (A) and average proportion ($M + SEM$) of Protected-geraniol diet consumed during a choice test of 24 hr (B), expressed by female observers in each experimental group ($n = 10$ in each group). Prot-: Protected (diet with a protective envelope). Comparisons by Fisher Pitman permutation tests for paired samples (A) and independent samples (B) ($^*p < 0.050$, n.s.: non-significant).

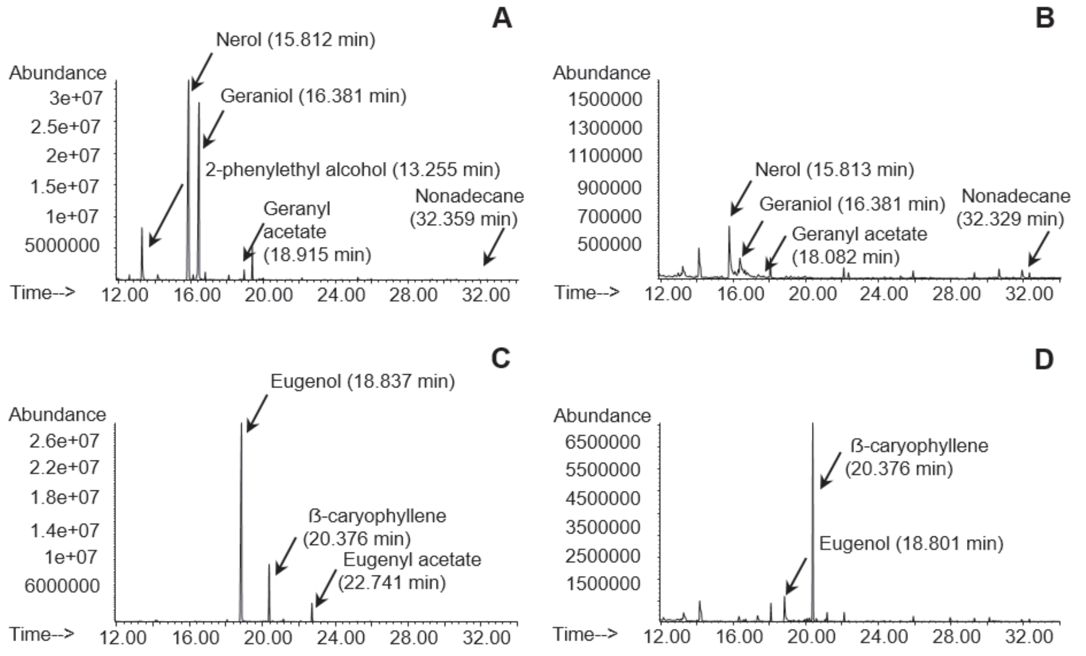

Figure 2.4 – Gas-chromatograms showing the detection of the odorant compounds present in Protected-Damascus rose diet sample (A), and in the feces sample of a female donor under the Protected-Damascus rose diet (B). Detection of the odorant compounds present in Protected-clove diet sample (C); and in the feces sample of a female donor under the Protected-clove diet (D).

Social phase

Female observers spent significantly more time on the dish carrying feces of a conspecific donor than on the control dish, regardless that their donor has consumed the Protected-Damascus rose diet ($M_{duration} \pm SEM$; dish with feces: 42 ± 5 s, control dish: 15 ± 2 s, $n = 10$) ($p = 0.01$, Cohen's $d = 1.55$) or the Protected-clove diet ($M_{duration} \pm SEM$; dish with feces: 41 ± 10 s, control dish: 16 ± 3 s, $n = 10$) ($p = 0.01$, Cohen's $d = 1.35$) (figure 2.5A).

Choice test

During the choice test of 24 hr, female observers which previously have been exposed to feces of an unfamiliar female donor under Protected-Damascus rose diet consumed significantly a higher proportion of Protected-Damascus rose diet than females previously exposed to feces of a donor under Protected-clove diet ($M_{proportion} \pm SEM$; Protected-Damascus rose group: 0.60 ± 0.11, $n = 10$, Protected-clove group: 0.18 ± 0.08, $n = 10$) ($p = 0.01$, Cohen's $d = 1.13$) (figure 2.5B).

Discussion

A crucial step allowing the establishment of the social transmission of food preference (STFP) results in the ability of the observer to match the diet odor perceived from the conspecific (or its products) and the odor of the diet itself. However, the conditions of the indirect STFP (via feces) require a transformation of food characteristics by the digestive system. This could imply specific characteristics of food items to be a good support for indirect STFP. Arakawa and his coworkers (2013) previously reported that indirect STFP was efficient when the information support was a food additive (cocoa or cinnamon powder). Here, we showed that a single odorant molecule as information support was not sufficient to clearly induce an indirect STFP in the house mouse.

Our results did not reveal the acquisition of the indirect STFP when the diets used differ by a single odorant molecule without protection (*Experiment 1*). Chemical analyses of synthetic standards and with samples of each diet

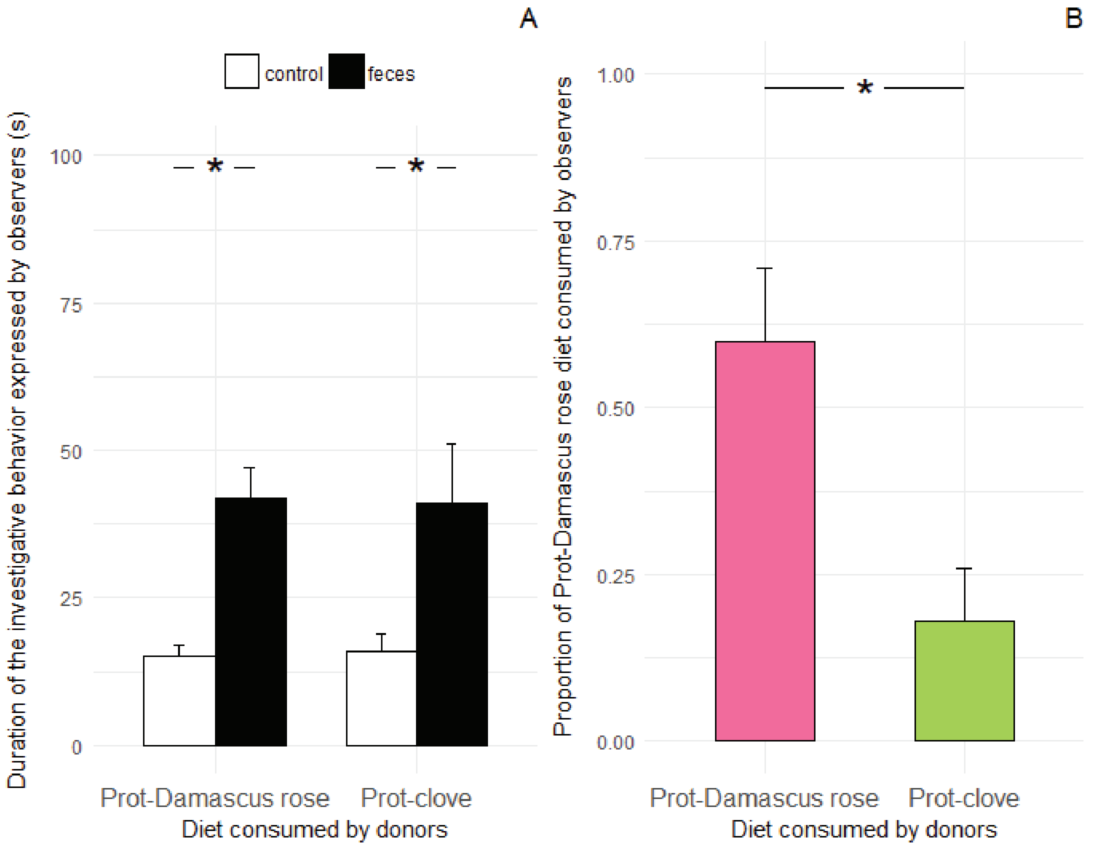

Figure 2.5 – Average duration ($M + SEM$) of investigative behavior on each dish presented during the social phase (A) and average proportion ($M + SEM$) of Protected-Damascus rose diet consumed during a choice test of 24 hr (B), expressed by female observers in each experimental group ($n = 10$ in each group). Prot-: Protected (diet with a protective envelope). Comparisons by Fisher Pitman permutation tests for paired samples (A) and independent samples (B) ($^*p < 0.050$).

(cinnamaldehyde diet and eugenol diet) confirmed that these molecules could be detected by SPME followed by GC-MS. Yet, single odorant molecules were not found in donor's feces by chemical analyses. This indicates that the digestive process altered the odorant information about the food in the donor's feces, thus limiting the establishment of the indirect STFP.

Michiels et al. (2008) showed in piglets that after an orally given dose, essential oils of cinnamaldehyde and eugenol were mainly and almost completely absorbed during the digestive process. Thus, it seems reasonable to think that, in our conditions, the absence of the molecules detection via chemical analysis was linked to an absence or a very low presence of these molecules in feces. However, the detection by the nose of a mouse could be more efficient than by GC-MS, and even a low quantity of the odor information could be perceived by mice. Although the STFP was not clearly established in these conditions, our results showed that the proportion of cinnamaldehyde diet in each experimental group was less than 0.50, which suggests a certain reluctance of observers to consume this diet whatever the diet of the donor. This effect appears to be stronger in the eugenol group than in the cinnamaldehyde group although the difference was not significant. It is therefore possible that single odorant molecules were still detected by the observers in the donor's feces. In any case, these conditions were not sufficient to allow the clear establishment of an indirect STFP and our results showed that digestive system is a possible constraint of indirect STFP by favoring the risk of alteration of information in feces.

This constraint is removed when the information allowing the identification of the diet is multiple. Indeed, the food additives used by Arakawa et al. (2013) included a large number of different odorant molecules and in these conditions, the indirect STFP was completely efficient. We obtained similar results using diets differing by other multiple odorants (*Experiment 3*). The presence of multiple odorants inside the diet could promote the conservation of some odorant characteristics of the food in feces, which could be sufficient for mice to match the odor from the feces with the food during the choice test. Indeed, although chemical analyses revealed the degradation of some odorant compounds originally present in diets (1 degraded compound over 4 in the Protected-Damascus rose diet and 1 over 3 compounds in the Protected-clove diet), the indirect STFP was clearly established in these conditions.

When the information characterizing the diet is reduced to a single odorant compound, the degradation or absorption of this one will definitively impair the matching between the odor present in feces and the odor of the diet itself. When the information was multiple, it may be expected that even if some of the compounds are degraded during the digestive process, the remaining odorant compounds could still allow to mice to make the association between the diet information perceived in feces and the diet itself. Thus, our results showed that, although the risk of degradation of information characterizing the diet was important during the indirect STFP, when the information was multiple, mice were able to use partial information to identify a food source.

According to these results, the preservation of a single odorant compound in the donor's feces should allow the establishment of the indirect STFP. However, even when we used diets that differed by a single odorant compound with a protection (*Experiment 2*), a clear indirect STFP was not established between female mice. This result was obtained despite chemical analyses revealed the presence of the single odorant compound in the donor's feces. This suggests that mice could perceive the single odorant compound during feces investigation but they did not use this information during food selection.

Consequently, another element that we highlighted in this study is that the multiplicity of odorant compounds characterizing the diet seems to be a necessary condition for the identification and discrimination of the food source. Effective communication requires that the receiver not only detects the presence of a cue but also discriminates significant cues (Wiley, 1983). It is assumed that in rodents, body odors, urine and feces convey numerous olfactory cues about traits (identity, sex, and species) and states (diet, age, health condition) of individuals (Ferkin et al., 1997; Hurst et al., 2001; Osada et al., 2003; Colombelli-Négrel & Gouat, 2006). The simultaneous perception of complex information relative to the donor in feces could interfere with the information about food, thus, the multiplicity of the food cues could be an essential element to favor its detection. In addition, differentiating two diets that possess a common general odor, based only on a single odorant compound can be a particularly difficult task. On the contrary, with a composite odor bouquet, each molecule can be matched between the donor odor and the food. In other words, the bouquet of molecules conveys redundant information about the same food source. In this situation, the mix of odorant compounds could allow more accurate assessment by the receiver, reducing discrimination errors (Bro-Jorgensen & Dabelsteen, 2008; Johnstone, 1996).

In similar conditions, Forestier et al. (In-Press) showed that direct STFP between female house mice was clearly established when the information support was a single odorant molecule. This difference in results suggests that the constraints observed during the indirect STFP are specific to this transmission pathway. The majority of food resources found in natural conditions corresponds to complex mixtures of several odorant compounds, which should reduce the constraints associated with the indirect STFP. However, the alteration of odorant information during the digestive process coupled with the necessity of a multiple cue characterizing the diet in feces could in some cases limit the acquisition of the indirect STFP. For example, if the mixture is processed with a configural perception (there are interactions between the mixture components that give unique properties to the mixture) (Pearce, 1987; Rudy & Sutherland, 1992; Gottfried, 2010), then, degradation of key components could alter the perception of the mixture and prevent the indirect STFP. Consequently, these constraints could have repercussions on the use by mice of these two paths of social influences under natural conditions. Indeed, while the direct STFP seems to be restricted by social constraints, it allows a more precise evaluation of the diets consumed by the conspecifics. Conversely, the indirect STFP reduces social constraints, but the identification of diets consumed by conspecifics seems more complex to achieve through the feces. Thus, by the constraints specific to each pathway, direct and indirect STFP can be complementary under natural conditions, each extending the conditions for the transmission of food information in rodents.

Supplemental materials

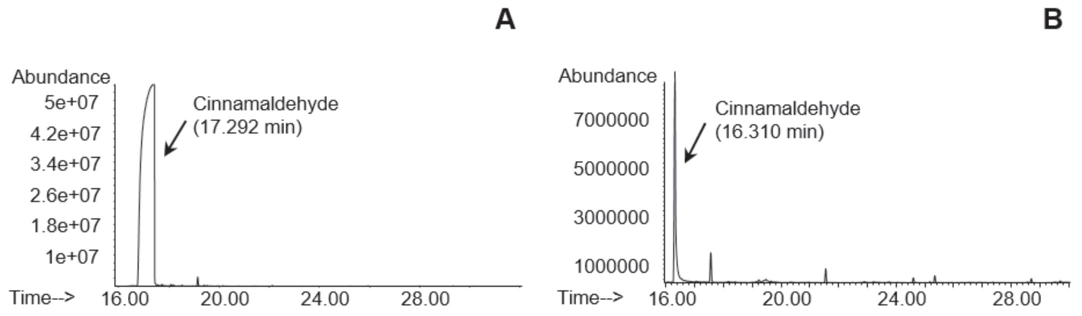

Figure 2.6 – Gas-chromatograms showing the detection of cinnamaldehyde in a sample of the synthetic standard (A) and in a sample of cinnamaldehyde diet (B).

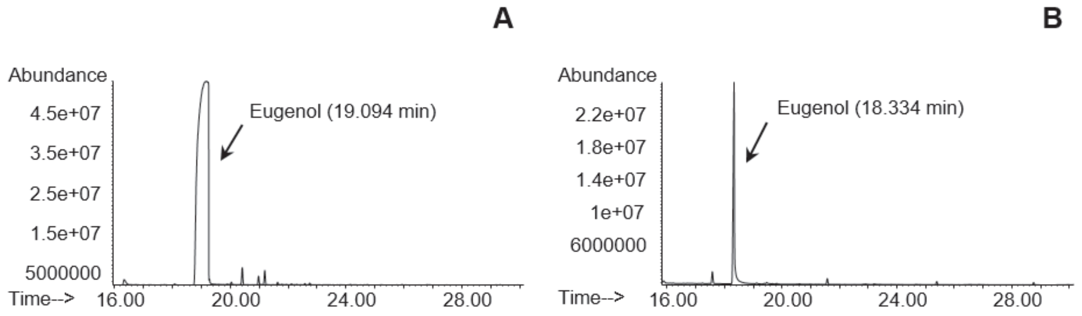

Figure 2.7 – Gas-chromatograms showing the detection of eugenol in a sample of the synthetic standard (A) and in a sample of eugenol diet (B).

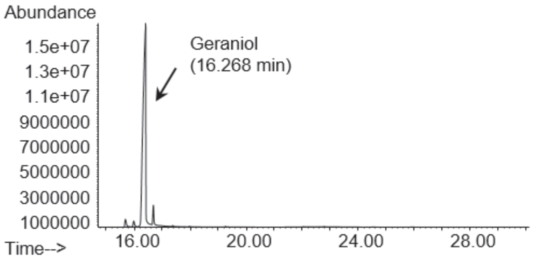

Figure 2.8 – Gas-chromatogram showing the detection of geraniol in a sample of the synthetic standard.

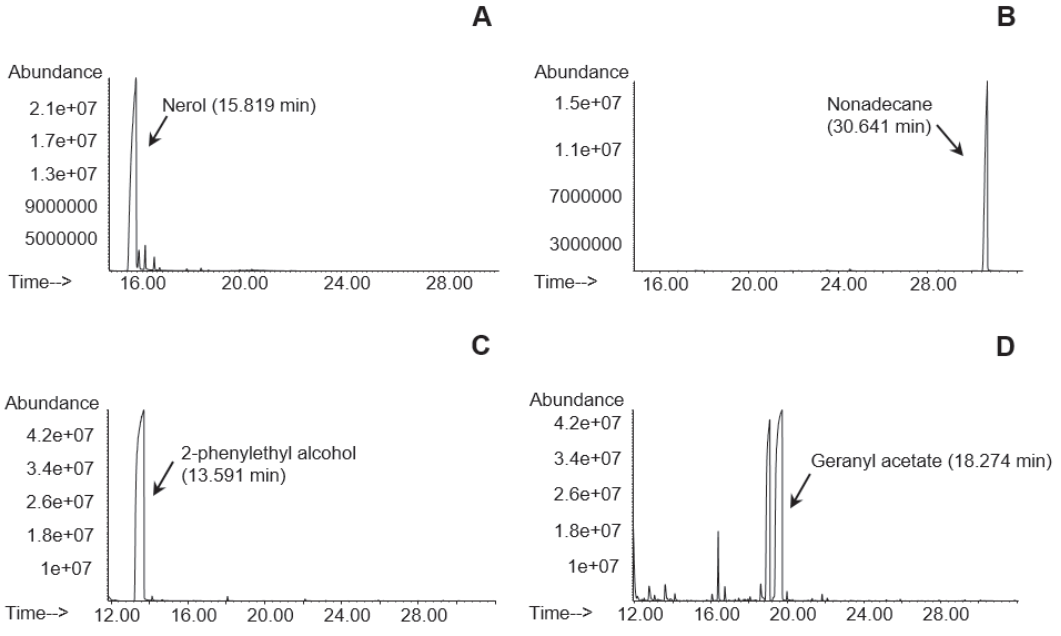

Figure 2.9 – Gas-chromatograms showing the detection of nerol (A), nonadecane (B), 2-phenylethyl alcohol (C) and geranyl acetate (D) in samples of synthetic standards.

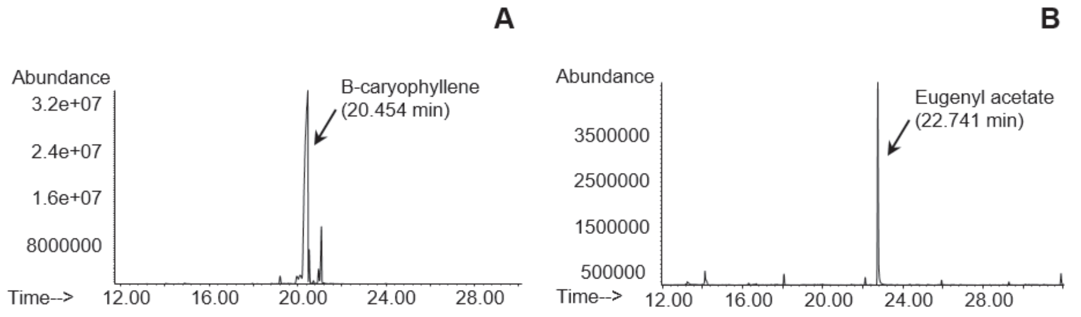

Figure 2.10 – Gas-chromatograms showing the detection of β-caryophyllene (A) and eugenyl acetate (B) in sample of synthetic standards.

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Chapter 3

Differences between male and female house mice in the use of food cues for the social transmission of food preference

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Social transmission of food preference via feces in house mice of wild origin: Who is a good provider of food cues?

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In preparation

Abstract

The social transmission of food preference (STFP) is a phenomenon that allows rodents to use food information perceived from their conspecifics to guide their own food choices. This social information can be collected via olfactory cues, during direct social interactions, or indirectly, via feces left in the environment by individuals. Although reducing the risks associated with a social interaction, feces convey also different type of information about traits and states of individuals which could affect the indirect STFP. Here, we evaluated in the house mouse, *Mus musculus domesticus* which social conspecifics could be used as providers of food cues for indirect STFP. Our results indicated that female mice were able to acquire an indirect STFP from feces of adult females, familiar or not and from feces of adult unfamiliar males. On the contrary, males did not establish an indirect STFP from feces of males, whether they are familiar or not, as well as those from unfamiliar females. Indirect STFP was only effective in males when the feces were those of an unfamiliar juvenile male. A prior habituation to the odor of an unfamiliar female, nevertheless, allowed the establishment of indirect STFP in males. However, the presence of feces of another adult male during the presentation of feces of a accustomed female precluded the acquisition of indirect STFP in males. This study suggested that in the context of the indirect STFP, females prioritize socio-olfactory information relative to food, whether food cues were not priority information for males. Under these conditions, females appear to be the best vectors for disseminating food information to the population. These results are discussed according to the socio-spatial organization of the species.

Keywords: attention, feces, olfaction, social information, rodents.

Introduction

The social transmission of food preference (STFP) is a phenomenon allowing rodents to enlarge their food repertoire at low risk by getting information on novel food sources from experienced conspecifics (Galef, 1986). Following a social encounter with a conspecific demonstrator that has recently consumed a novel food item, rodents such as rats and mice will show afterwards a substantially enhanced preference for the same type of food as ingested by their demonstrator (referred to as 'direct STFP' hereafter) (Galef & Wigmore, 1983; Posadas-Andrews & Roper, 1983; Valsecchi & Galef, 1989). This behavior can also be promoted indirectly in mice after the investigation of feces of a donor conspecific (referred to as 'indirect STFP' hereafter) (Arakawa et al., 2013). This second way of STFP offers the advantage of reducing the constraints associated with the presence of a conspecific, particularly in the case of social intolerance (Forestier et al., In-Press).

In addition to provide information about new food sources, feces convey also information about traits (e.g. identity, sex, and species) and states (i.e. reproductive status, age, health condition) of individuals (Brown, 1979; Colombelli-Négrel & Gouat, 2006; Hurst et al., 2001; Osada et al., 2003). Because all these different kinds of information are perceived simultaneously in a unique source (i.e. olfactory marks), some of them could be integrated in priority making them more relevant at the expense of food information and consequently impair the acquisition of the indirect STFP. The relevance of a type of information could be modulated by the different biological needs and priorities of males and females and the food cues present in feces could be neglected or, on the contrary, privileged, over the other cues characterizing the conspecific. To test this hypothesis, we proposed to identify which social conspecifics could be used as providers of food cues for indirect STFP in the house mouse, *Mus musculus domesticus*.

In the house mouse, related females tend to live on the territory of a male and raise their young together (König & Lindholm, 2012). They are relatively intolerant toward other females which represent potential competitors for resources. Females mate with their territorial male but can also mate with other territorial or peripheral males (Rolland et al., 2003; Thonhauser et al., 2014). The settlement of a female in a male home range then depends more on the resources it contains than on the intrinsic qualities of the male owner. As for all mammalian females, food resource is paramount concern for female house mice to ensure the proper functioning of their complete reproductive cycle (Hamilton & Bronson, 1985; Speakman, 2008). Because food resources are often limited and variable over time in their environment, enlarging their food repertoire should limit the risk of food shortage. We then hypothesized that, for females, food cues should have priority over other cues present in feces regardless of the characteristics of the donor conspecific. Male and female conspecifics should then be good providers of food cues for indirect STFP in females.

The socio-spatial organization of the house mouse relies essentially on the existence of territorial males structuring the use of space (Hurst, 1990a). Competition between adult males is high and is reflected by the numerous attacks by territorial males against neighbors and unfamiliar male intruders (Rowe & Redfern, 1969; Hurst, 1990a, 1990b, 1990c; Latham & Mason, 2004). Olfactory marks play a major role in communication between males and scent marking is a fundamental component of territorial behavior (Hurst, 1990a; Gosling & Roberts, 2001; Hurst & Beynon, 2004). Males should therefore prioritize information about potential intruders, whatever wandering and unfamiliar males, or usual male neighbors. Juvenile and female individuals, on the other hand, do not represent a threat for territorial males and could be good providers of food cues for indirect STFP in males. Nevertheless, unlike females, the reproductive potential of males is, to a large extent, unaffected by the availability of food (Hamilton & Bronson, 1985) and access to new females is a key element of their reproductive success (Wolff & Sherman, 2007). In this case, males should prioritize information about potential sexual partners and the indirect STFP could be impaired when the donor is an unfamiliar female.

To test our hypotheses, the acquisition of indirect STFP was tested in male and female adult mice. In a first experiment the donor and the observer were of the same sex but the donor was either a familiar or an unfamiliar conspecific. Because an adult male represents a threat for other males and that this information could be the main cause of the impairment of the indirect STFP, we also tested in males, the efficiency of an unfamiliar juvenile male as donor.

In a second experiment, we compared the establishment of indirect STFP between male and female mice when the donor was an unfamiliar conspecific of the opposite sex.

In the preceding experiments the characteristics of the donor was predicted to play a major role in males preventing an effective STFP. To disentangle whether this result would be due to the novelty or to the strong functional concerns of the donor, we tested in a third experiment the effect of a prior habituation to the odor of an unfamiliar donor on the effectiveness of the STFP. These conditions were tested only in males either with an unfamiliar female donor or with an unfamiliar male donor.

In a last experiment, we tested in males whether the presence of the odor from a potential competitor was sufficient to alter the acquisition of food information provided by another non-competing conspecific.

Methods

Animals and breeding conditions

The animals used in this study were house mice, *Mus musculus domesticus*, descendants from animals of wild origin provided and bred for more than ten generations at the laboratory RS2GP of VetAgro Sup Lyon (France). The mice were bred in our laboratory for seven generations with addition of wild animals captured at different sites in France, in the Die region (Vachères en Quint 44.789720 N, 5.259654 E, Montlaur en Diois 44.789720 N, 5.259654 E) and in the Beaujolais region (Chambost-Allières 46.012944 N, 4.481324 E).

We used 347 adult male and female mice ($M_{age} \pm SEM$: 181 ± 3 d) and 11 juvenile mice ($M_{age} \pm SEM$: 30 ± 1 d)(detailed in table 3.1).

	Relation Observer → Donor	**Observers** (breeding pairs)	**Donors** (breeding pairs)
Exp. 1	♀→ Fam ♀	$N = 26$ (8)	$N = 15$ (8)
	♀→ NF ♀	$N = 20$ (5)	$N = 16$ (4)
	♂→ Fam ♂	$N = 21$ (9)	$N = 10$ (9)
	♂→ NF ♂	$N = 20$ (13)	$N = 22$ (13)
	♂→ NF juvenile ♂	$N = 20$ (8)	$N = 11$ (3)
Exp. 2	♀→ NF ♂	$N = 20$ (11)	$N = 16$ (10)
	♂→ NF ♀	$N = 20$ (11)	$N = 10$ (7)
Exp. 3	♂→ Hab ♂	$N = 20$ (14)	$N = 16$ (7)
	♂→ Hab ♀	$N = 20$ (12)	$N = 13$ (7)
Exp. 4	♂→ Hab ♀ + NF ♂	$N = 20$ (9)	$N = 12$ (4) + $N = 10$ (7)

Table 3.1 – Number of mice and number of breeding pairs used in each experiment. Fam: familiar and related individuals; NF: unfamiliar and unrelated individuals; Hab: with habituation phase

The room in which the mice resided was environmentally controlled on a 14:10-h-light-dark cycle (19:00-9:00-h lighting) at a temperature of 20 ± 2 °C and relative humidity of 50-60%. During the dark phase, the room was lit by a red light (two neon tubes, 35 W) allowing observation by the experimenter. The mice were housed in standard polycarbonate cages (365 × 207 × 140 mm) with a bedding of wood shavings (Special Diet Services, Witham, Essex, U.K.) and cotton as nesting material. Pelleted food (type M20, Special Diet Services, Witham, Essex, U.K.) and water were supplied *ad libitum*. The mice were weaned at 21 days of age and were placed in same-sex sibling groups one week later. At least one week before the experiment, animals were transferred to the experimental room. Females were placed in a new cage with a same-sex sibling and males were isolated. Individuals were marked by hair clipping when necessary and were tested individually.

Diets

Diets used in these experiments derived from a bait originally designed to control rodent pest populations. The diets were specifically manufactured for these experiments by Liphatech (Liphatech S.A., Pont du Casse, Lot et Garonne, France). The bait used was an artificial paste with high lipid content and did not contain any rodenticide. The two diets were of the same composition and only differed by the addition of a flavored powder unsweetened: either 2% of cinnamon powder (referred to as ‘cinnamon diet’ hereafter) or 4% of cocoa powder (referred to as ‘cocoa diet’ hereafter). These products are used for human food consumption.

Experimental procedure

The general paradigm used in this study was based on the different procedures developed to test the social transmission of food preference (STFP) in rats and mice where each experiment encompassed a social phase followed by a choice test (Arakawa et al., 2013; Galef & Wigmore, 1983; Posadas-Andrews & Roper, 1983; Valsecchi & Galef, 1989). Elements that may vary during the social phase depending on the experiments are presented in Figure 3.1. During the social phase, a naive observer was confronted with social information about a given diet through the presentation of the feces of a conspecific donor. Each experiment included two groups of animals differing in the nature of the diet (cinnamon diet or cocoa diet) experienced by the donor (cinnamon group and cocoa group). During the choice test, the observer was confronted with the two diets. The STFP was considered as being acquired when the two groups differed significantly in their food preference.

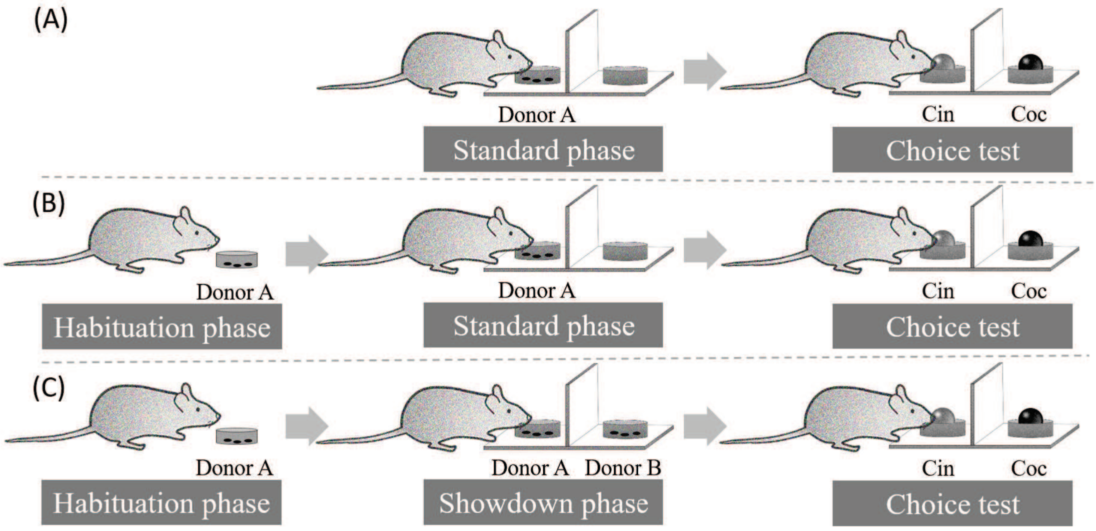

Figure 3.1 – Different experimental designs used in this study during the social phase. (A) *Experiment 1* and *Experiment 2* (B) *Experiment 3* and *Experiment 4* (C) *Experiment 4*. Standard phase: feces presentation of the donor A under a new diet. Habituation phase: feces presentation of the donor A under the standard diet. Showdown phase: simultaneous presentation of feces of the donor A under a new diet and of the donor B under the standard diet. Cin: cinnamon diet; Coc: cocoa diet

Social phase

Standard phase (*Experiment 1* and *Experiment 2*): feces presentation of a donor under a new diet Donors were isolated in a clean standard polycarbonate cage with a bedding of wood shavings and cotton as nesting material. They were given 9 g of one of the two diets simultaneously with the standard diet during 72 hr. The consumption of the diet was quantified at the end of this period (table 3.2). When a donor did not consume the proposed diet, it was removed from the experiment (*Experiment 1*: 2 males in cinnamon group and 2 juvenile males in each group; *Experiment 2*: 1 male in cinnamon group and 2 females in each group).

The feces of donors were collected during the lit period (0.20 ± 0.02 g per sample). Because the artificial paste was colored and also colored the feces,

	Relation	**Mean consumption ± standard error (g)**	
	Observer → Donor	Cinnamon diet	Cocoa diet
Exp. 1	♀→ Fam ♀	4.86 ± 1.01	7.25 ± 0.59
	♀→ NF ♀	8.17 ± 0.49	8.69 ± 0.24
	♂→ Fam ♂	6.37 ± 0.88	5.58 ± 0.96
	♂→ NF ♂	7.09 ± 0.95	8.44 ± 0.31
	♂→ NF juvenile ♂	6.28 ± 1.57	6.86 ± 1.37
Exp. 2	♀→ NF ♂	7.34 ± 0.80	8.37 ± 0.46
	♂→ NF ♀	8.51 ± 0.41	8.36 ± 0.59
Exp. 3	♂→ Hab ♂	8.06 ± 0.78	8.82 ± 0.14
	♂→ Hab ♀	5.33 ± 0.98	6.56 ± 0.92
Exp. 4	♂→ Hab ♀ + NF ♂	8.81 ± 0.13	8.56 ± 0.44

Table 3.2 – Average consumption of donors after 72 hr of feeding period (9 g of cocoa or cinnamon diet simultaneously with the standard diet) for each experiment. Fam: familiar and related individuals; NF: unfamiliar and unrelated individuals; Hab: with habituation phase

this color indicator was used to collect the feces that were excreted after diet consumption. Each sample was then placed in a sealed freezer bag and placed at −20 °C until required. On the day of the experiment, the donors' feces were thawed 30 min before the beginning of the feces presentation. Feces were placed in a clean Petri dish fixed on a support (figure 3.1) together with another clean Petri dish (control) to verify that the observer perceived the odorant stimulus (Colombelli-Négrel & Gouat, 2006). The position of each dish on the support (left/right) was randomly assigned and balanced across trials. The feces presentation occurred during the dark period. The observer was placed in a clean cage covered by a transparent tray and had five min to acclimate to the cage. A transparent tray was placed on the cage to prevent observers from escaping, and to allow observation. The support with the dishes was introduced into the cage. The feces presentation lasted ten min starting with the first contact of the mouse with the support. Investigation time of each dish was measured from a video-recording of the experiment (Sony FDR-AX100E). At the end of the feces presentation, the support was removed and the observer was transferred to a clean test cage. The choice test (see below) began five min later.

Habituation phase (*Experiment 3* and *Experiment 4*): feces presentation of a donor under the standard diet Twenty-four hr before the beginning of the feces presentation, observers were habituated to the odor of their donor when this one was under standard diet. For this, the preparation of the donors consisted of isolating them in a clean cage with a bedding of wood shavings, cotton, standard diet and water supplied *ad libitum* for 24 hr. At the end of this period, feces were collected (0.20 ± 0.02 g per sample) and placed in a sealed freezer bag at −20 °C until required. Twenty-four hr before the beginning of the test, the feces samples were thawed and feces were placed in a clean dish. The dish was inserted into the observer's home cage and left until the start of the test. The test procedure was then the same as that described above. At the end of the experiment, the observer was placed in a new clean cage.

Showdown phase (*Experiment 4*): simultaneous presentation of feces of a donor under the standard diet and a donor under a new diet This phase consisted to test the influence of the presence of feces of a potential competitor on the acquisition of the STFP. The procedure for collecting feces from the donors was the same as that described for donors used in the habituation phase. On the day of the experiment, the observer was placed in a clean cage covered by a transparent tray. From the beginning of the experiment, the Petri dish containing the feces of a potential competitor donor under standard diet was introduced into the cage. After five minutes, the support with the dishes containing the feces of a non-competing donor was introduced into the cage and placed to the opposite side in the cage. The presentation of the feces lasted ten minutes starting with the first contact of the mouse with the support. At the end of the feces presentation, the observer was transferred to a clean test cage. The choice test (see below) began five minutes later.

Choice test

For each experiment, the procedure of choice test was the same. A 3 g sample of each diet was placed in a Petri dish to limit the dispersion of unconsumed food. The two Petri dishes were fixed to a support of the same type as the one shown in the figure 3.1 and then placed inside the test cage. The position (left or right) of each diet was randomly assigned and balanced. A transparent tray was placed on the cage to prevent escape. The support with the diets was introduced into the test cage. The test lasted one hour from the first contact of the mouse with the support. At the end of the test, the remaining food was collected carefully inside the cage and the amount of unconsumed food was measured using a balance accurate to ± 0.02 g. When the test was finished at 1 hr, the observer was returned to its home cage. When it was extended to 24 hr, the diets were therefore reintroduced into the cage. At 1 hour, the transparent tray was replaced by a grid containing water and standard food *ad libitum*. Cotton for nesting material was also added to the observer's cage. At the end of the 24 hr of test, the remaining food was collected and weighed and the observer was returned to its home cage.

In *Experiment 1*, the duration of the choice test (1 hr) was the same as that used in the study highlighting the indirect STFP (Arakawa et al., 2013). In the following experiments because the animals tested were more reluctant to consume at least one of the two diets at 1 hr, we extended the test to 24 hr in order to establish whether the STFP was acquired. This duration corresponded to the usual duration of previous studies working on direct STFP (Galef & Wigmore, 1983; Posadas-Andrews & Roper, 1983; Valsecchi & Galef, 1989).

Ethics note

Experimental procedures were approved by the French ethics committee "Charles Darwin C2EA 05" (reference number 04355.02). This study did not require euthanasia of mice at the end of experiments and subjects were therefore retained for later use.

Data analysis

The data collection and analysis were done blind to group identity to remove any source of unintentional bias. Because of the small number of animals in each group ($N < 15$), we used non parametric statistics. The results were significant when $p \leq 0.05$ and the data were reported by their mean (M) and standard error (SEM). We also reported the effect size by using the Cohen's d value. All statistical comparisons were performed with the software StatXact (Cytel Software Corporation, 2010).

To verify the interest of the observers for the feces presented during the social phase, we compared the duration of investigative behavior expressed by observers for each dish present on the device. For this, we used Permutation tests for paired samples. For technical problems, the investigation time of a certain number of observers could not be accurately measured during the social phase and in this case they were removed from the social phase analyzes but conserved for analyzes of the choice test.

The acquisition of the STFP was assessed by comparing the proportion of cinnamon diet consumed by the observers of the two experimental groups (cinnamon group vs. cocoa group) during the choice test (Galef & Wigmore, 1983). The proportion of cinnamon diet corresponded to the ratio of the quantity of cinnamon diet consumed over the total consumption (total quantity consumed) of both diets. When an observer did not consume any diet during the choice test, it was removed from the statistical analysis. We used Permutation tests for independent samples.

Results

Experiment 1: indirect STFP between familiar and unfamiliar conspecifics of same-sex

Females

Social phase The time spent by females on the Petri dish containing the feces of a familiar female donor was significantly higher than on the control dish, as donors have consumed the cinnamon diet ($M_{duration} \pm SEM$; dish with feces: 50 ± 8 s, control dish: 17 ± 3 s, $n = 12$) ($p = 0.001$, Cohen's $d = 1.23$) or the cocoa diet ($M_{duration} \pm SEM$; dish with feces: 43 ± 7 s, control dish: 15 ± 3 s, $n = 14$) ($p = 0.0001$, Cohen's $d = 1.15$).

Similarly, females spent more time investigating the Petri dish containing the feces of an unfamiliar female donor than the control dish, whatever they have been consuming the cinnamon diet ($M_{duration} \pm SEM$; dish with feces: 65 ± 8 s, control dish: 29 ± 3 s, $n = 10$) ($p = 0.004$, Cohen's $d = 1.42$) or the cocoa diet ($M_{duration} \pm SEM$; dish with feces: 48 ± 5 s, control dish: 21 ± 3 s, $n = 10$) ($p = 0.002$, Cohen's $d = 1.45$).

Choice test When the social transmission of food preference (STFP) was tested between familiar females, six observers did not consume any diet during the choice test of 1 hr and were removed from the analysis.

Females, having investigate the feces of a familiar female donor under cinnamon diet, ate significantly a higher proportion of cinnamon diet than females with a donor under cocoa diet ($M_{proportion} \pm SEM$; cinnamon group: 0.73 ± 0.09, $n = 10$, cocoa group: 0.38 ± 0.11, $n = 10$) ($p = 0.045$, Cohen's $d = 0.89$) (figure 3.2A).

In the same way, when exposed to feces of an unfamiliar female donor which consumed cinnamon diet, female observers ate significantly a higher proportion of the cinnamon diet than females with a donor under cocoa diet ($M_{proportion} \pm$

SEM; cinnamon group: 0.81 ± 0.08, $n = 10$, cocoa group: 0.49 ± 0.11, $n = 10$) ($p = 0.03$, Cohen's $d = 0.94$) (figure 3.2B).

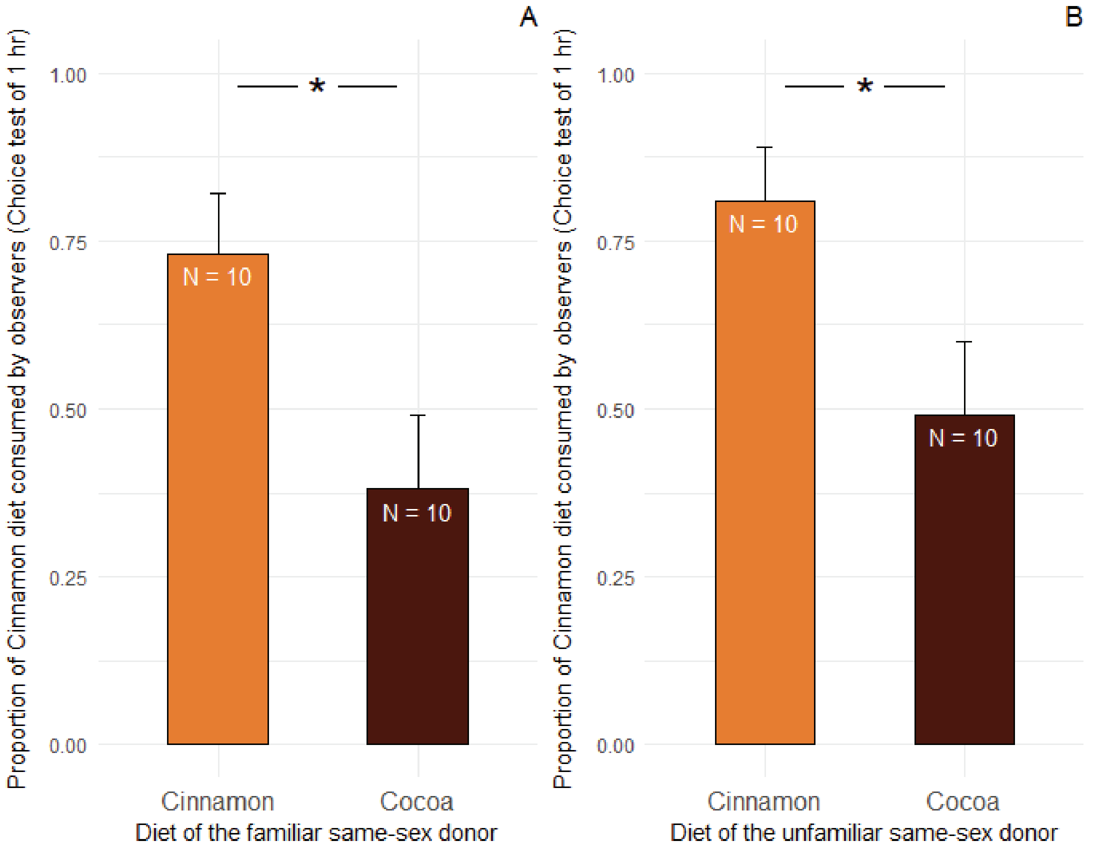

Figure 3.2 – Average proportion ($M + SEM$) of cinnamon diet consumed during a choice test of 1 hr by female observers in each experimental group after the presentation of feces of a familiar female donor (A) and of an unfamiliar female donor (B) under cinnamon or cocoa diet. Comparisons by Fisher Pitman permutation tests for independent samples (*$p < 0.05$).

Males

Adult male donors

Social phase The time spent by males on the Petri dish containing the feces of a familiar male donor was significantly higher than on the control dish, whatever they have been consuming the cinnamon diet ($M_{duration} \pm SEM$; dish with feces: 55 ± 7 s, control dish: 24 ± 4 s, $n = 10$) ($p = 0.006$, Cohen's $d = 1.34$) or the cocoa diet ($M_{duration} \pm SEM$; dish with feces: 47 ± 11 s, control dish: 14 ± 3 s, $n = 10$) ($p = 0.006$, Cohen's $d = 1.12$).

Similarly, males spent significantly more time on the Petri dish containing the feces of an unfamiliar male donor than on the control dish, as donors have consumed the cinnamon diet ($M_{duration} \pm SEM$; dish with feces: 72 ± 6 s, control dish: 24 ± 3 s, $n = 9$) ($p = 0.004$, Cohen's $d = 1.67$) or the cocoa diet ($M_{duration} \pm SEM$; dish with feces: 73 ± 13 s, control dish: 20 ± 2 s, $n = 10$) ($p = 0.002$, Cohen's $d = 1.34$).

Choice test Male observers, having investigate the feces of a familiar male donor under cinnamon diet, did not consume significantly a higher proportion of cinnamon diet than males with a donor under cocoa diet ($M_{proportion} \pm SEM$; cinnamon group: 0.51 ± 0.14, $n = 10$, cocoa group: 0.52 ± 0.11, $n = 10$) ($p = 0.96$, Cohen's $d = 0.03$) (figure 3.3A).

Similarly, when exposed to feces of an unfamiliar male donor which ate cinnamon diet, males did not consume significantly a higher proportion of the cinnamon diet than males with a donor under cocoa diet ($M_{proportion} \pm SEM$; cinnamon group: 0.70 ± 0.09, $n = 10$, cocoa group: 0.59 ± 0.13, $n = 10$) ($p = 0.53$, Cohen's $d = 0.30$) (figure 3.3B).

Juvenile male donors

Social phase Males spent significantly more time on the Petri dish containing the feces of a juvenile male donor than on the control dish, as donors have consumed the cinnamon diet ($M_{duration} \pm SEM$; dish with feces: 78 ± 13 s, control dish: 24 ± 5 s, $n = 10$) ($p = 0.004$, Cohen's $d = 1.30$) or the cocoa diet ($M_{duration} \pm SEM$; dish with feces: 99 ± 19 s, control dish: 17 ± 3 s, $n = 10$) ($p = 0.004$, Cohen's $d = 1.37$).

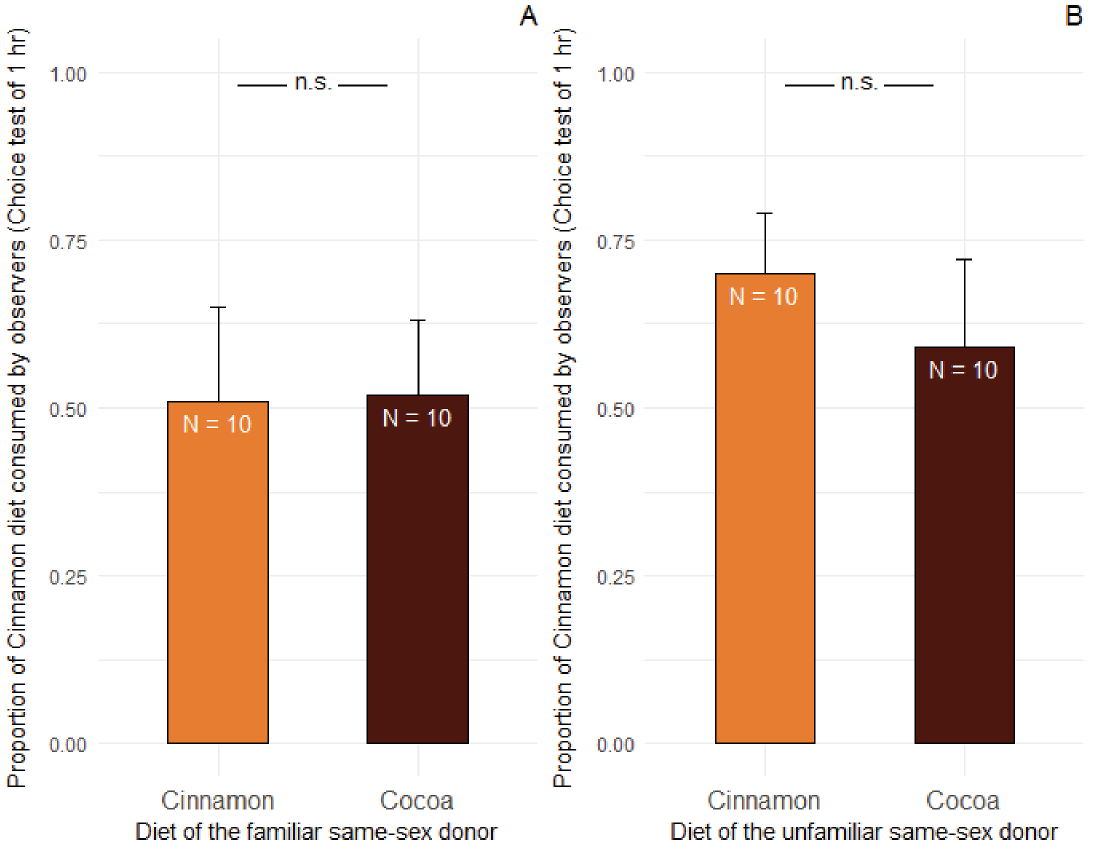

Figure 3.3 – Average proportion ($M + SEM$) of cinnamon diet consumed during a choice test of 1 hr by male observers in each experimental group after the presentation of feces of a familiar male donor (A) and of an unfamiliar male donor (B) under cinnamon or cocoa diet. Comparisons by Fisher Pitman permutation tests for independent samples (n.s.: non-significant).

Choice test One observer did not consume any diet during the choice test of 1 hr and was removed from the analysis.

Males, having investigate the feces of an unfamiliar juvenile male donor under cinnamon diet, ate significantly a higher proportion of cinnamon diet than males with a donor under cocoa diet ($M_{proportion} \pm SEM$; cinnamon group: 0.85 ± 0.10, $n = 10$, cocoa group: 0.48 ± 0.11, $n = 9$) ($p = 0.03$, Cohen's $d = 1.00$) (figure 3.4).

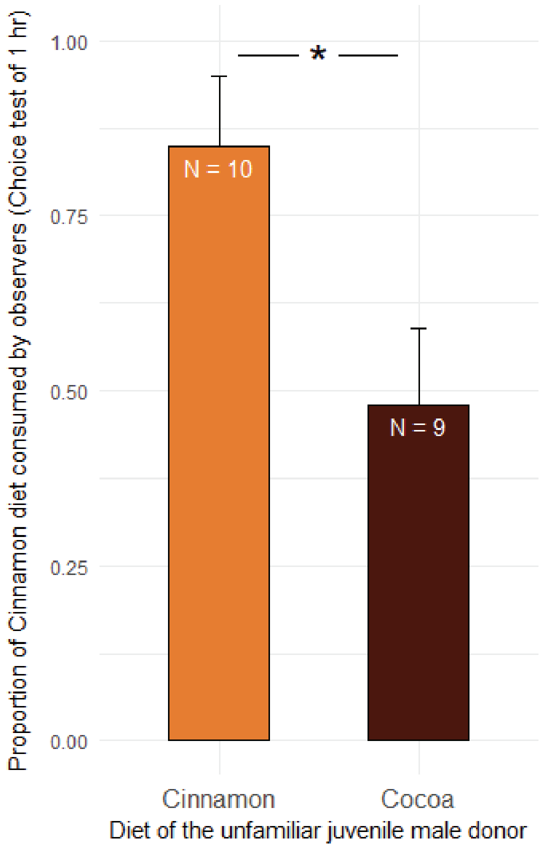

Figure 3.4 – Average proportion ($M + SEM$) of cinnamon diet consumed during a choice test of 1 hr by adult male observers in each experimental group after the presentation of feces of an unfamiliar juvenile male donor under cinnamon or cocoa diet. Comparisons by Fisher Pitman permutation tests for independent samples ($^*p < 0.05$).

Experiment 2: indirect STFP between unfamiliar conspecifics of opposite-sex

Females

Social phase The time spent by females on the Petri dish containing the feces of an unfamiliar male donor was significantly higher than on the control dish, as donors have consumed the cinnamon diet ($M_{duration} \pm SEM$; dish with feces: 56 ± 7 s, control dish: 24 ± 5 s, $n = 9$) ($p = 0.008$, Cohen's $d = 1.29$) or the cocoa diet ($M_{duration} \pm SEM$; dish with feces: 68 ± 16 s, control dish: 18 ± 4 s, $n = 10$) ($p = 0.002$, Cohen's $d = 1.14$).

Choice test Ten observers did not consume any diet during the choice test of 1 hr and were removed from the analysis of 1 hr test. However, after 24 hr of choice test, these same observers consumed at least one of the two diets and were thus reintegrated for the analysis of the 24 hr test.

The proportion of cinnamon diet consumed during the choice test of 1 hr did not differ between the two experimental groups ($M_{proportion} \pm SEM$; cinnamon group: 0.82 ± 0.10, $n = 6$, cocoa group: 0.68 ± 0.12, $n = 4$) ($p = 0.67$, Cohen's $d = 0.42$) (figure 3.5A).

However, during the choice test of 24 hr, all the observers consumed at least one of the two diets. Females which previously investigated feces of an unfamiliar male donor under cinnamon diet consumed a significantly higher proportion of cinnamon diet than females having previously investigated feces of a donor under cocoa diet ($M_{proportion} \pm SEM$; cinnamon group: 0.59 ± 0.09, $n = 10$, cocoa group: 0.29 ± 0.09, $n = 10$) ($p = 0.03$, Cohen's $d = 0.93$) (figure 3.5B).

Males

Social phase Males spent significantly more time on the Petri dish containing the feces of an unfamiliar female donor than on the control dish, whatever they

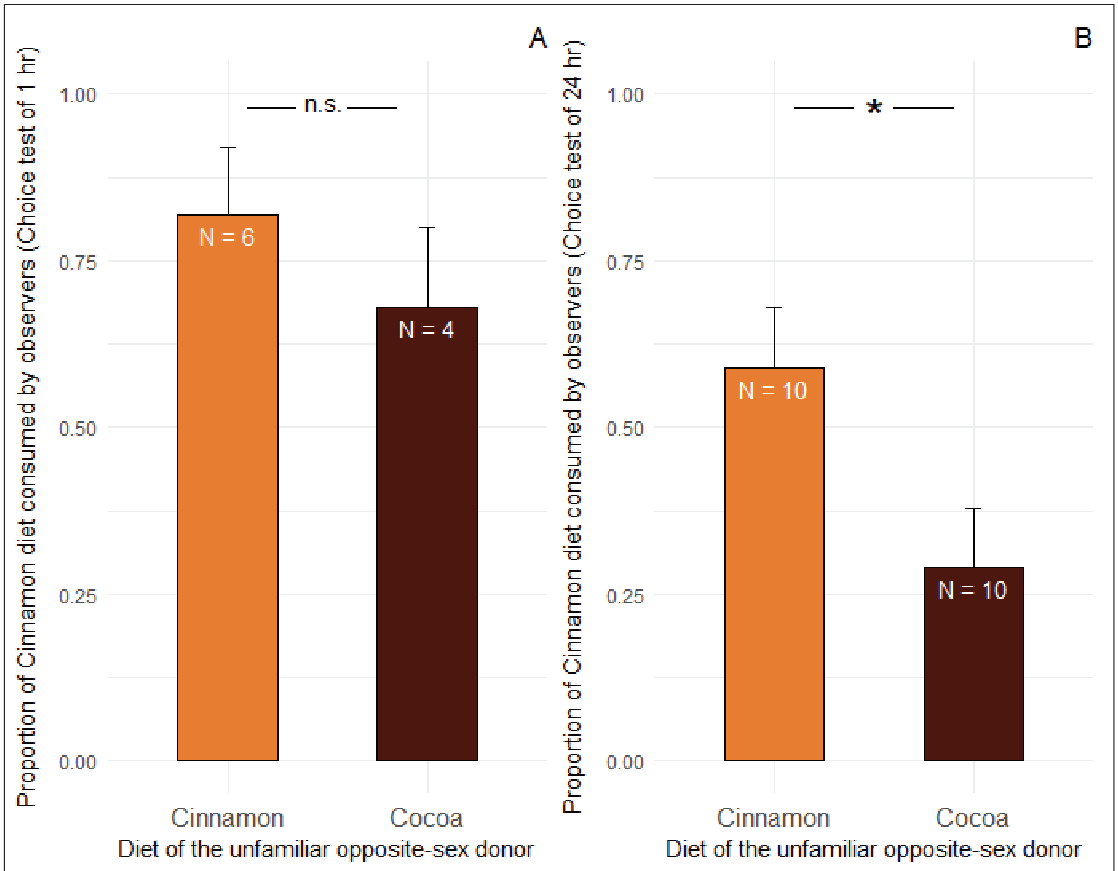

Figure 3.5 – Average proportion ($M + SEM$) of cinnamon diet consumed during a choice test of 1 hr (A) and of 24 hr (B) by female observers in each experimental group after the presentation of feces of an unfamiliar male donor under cinnamon or cocoa diet. Comparisons by Fisher Pitman permutation tests for independent samples (*$p < 0.05$, n.s.: non-significant).

have been consuming the cinnamon diet ($M_{duration} \pm SEM$; dish with feces: 87 ± 15 s, control dish: 19 ± 4 s, $n = 10$) ($p = 0.001$, Cohen's $d = 1.40$) or the cocoa diet ($M_{duration} \pm SEM$; dish with feces: 124 ± 18 s, control dish: 23 ± 3 s, $n = 10$) ($p = 0.002$, Cohen's $d = 1.55$).

Choice test Three observers did not consume any diet during the choice test of 1 hr and were removed from the analysis of 1 hr test. Nevertheless, after 24 hr of choice test, these same observers consumed at least one of the two diets and were thus reintegrated for the analysis of the 24 hr test.

The proportion of cinnamon diet consumed during the choice test of 1 hr did not reach the significance between the two experimental groups ($M_{proportion} \pm SEM$; cinnamon group: 0.66 ± 0.09, $n = 8$, cocoa group: 0.49 ± 0.13, $n = 9$) ($p = 0.33$, Cohen's $d = 0.48$) (figure 3.6A).

A similar result was obtained during the choice test of 24 hr ($M_{proportion} \pm SEM$; cinnamon group: 0.58 ± 0.12, $n = 10$, cocoa group: 0.39 ± 0.08, $n = 10$) ($p = 0.20$, Cohen's $d = 0.58$) (figure 3.6B).

Experiment 3: effect of modulation of social information characterizing the donor on indirect STFP

Habituation to unfamiliar male donors

Social phase During the social phase, males spent significantly more time on the Petri dish containing the feces of the accustomed male donor than on the control dish, whatever they have been consuming the cinnamon diet ($M_{duration} \pm SEM$; dish with feces: 50 ± 5 s, control dish: 19 ± 3 s, $n = 8$) ($p = 0.008$, Cohen's $d = 1.60$) or the cocoa diet ($M_{duration} \pm SEM$; dish with feces: 52 ± 8 s, control dish: 15 ± 3 s, $n = 10$) ($p = 0.002$, Cohen's $d = 1.38$).

Choice test Eight observers did not consume any diet during the choice test of 1 hr and were removed from the analysis of 1 hr test. Nevertheless, after 24 hr

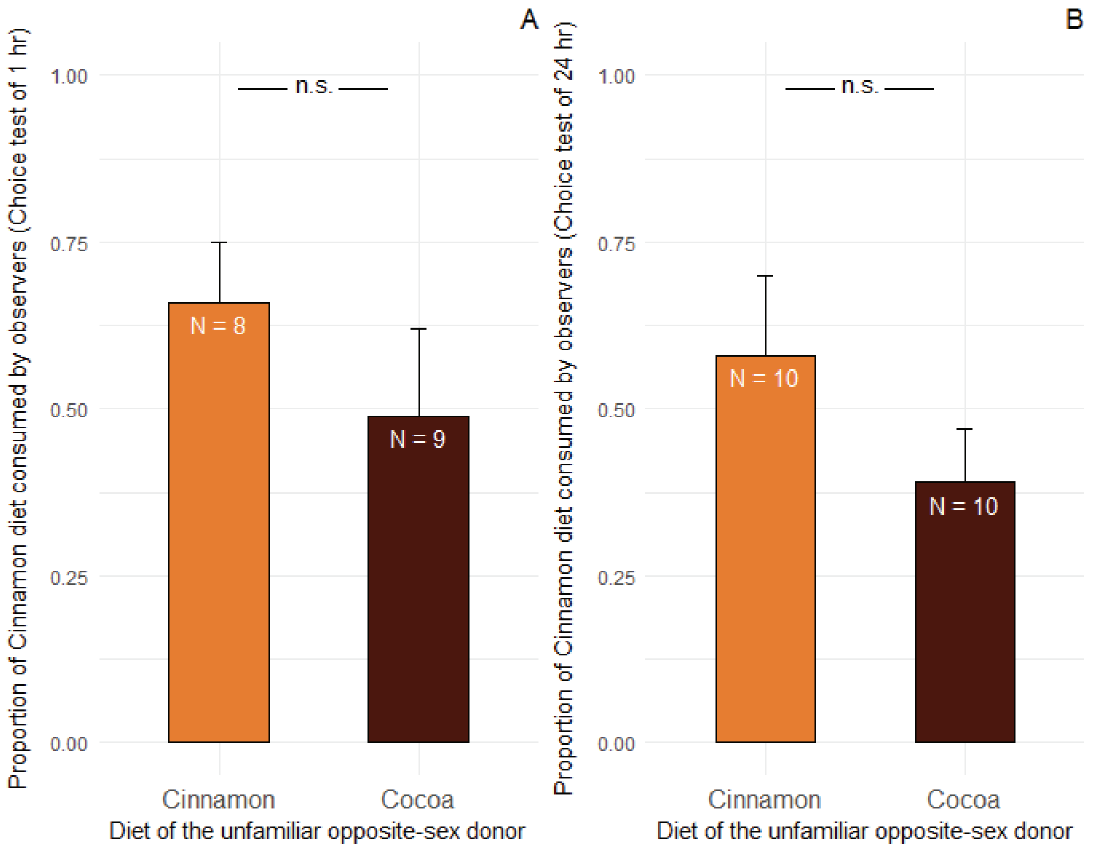

Figure 3.6 – Average proportion ($M + SEM$) of cinnamon diet consumed during a choice test of 1 hr (A) and of 24 hr (B) by male observers in each experimental group after the presentation of feces of an unfamiliar female donor under cinnamon or cocoa diet. Comparisons by Fisher Pitman permutation tests for independent samples (n.s.: non-significant).

of choice test, these same observers consumed at least one of the two diets and were thus reintegrated for the analysis of the 24 hr test.

The proportion of cinnamon diet consumed during the choice test of 1 hr did not differ significantly between the two experimental groups ($M_{proportion} \pm SEM$; cinnamon group: 0.51 ± 0.12, $n = 6$, cocoa group: 0.21 ± 0.06, $n = 6$) ($p = 0.12$, Cohen's $d = 0.90$) (figure 3.7A).

A similar result was obtained during the choice test of 24 hr ($M_{proportion} \pm SEM$; cinnamon group: 0.36 ± 0.09, $n = 10$, cocoa group: 0.38 ± 0.11, $n = 10$) ($p = 0.85$, Cohen's $d = 0.09$) (figure 3.7B).

Habituation to unfamiliar female donors

Social phase The time spent by males on the Petri dish containing the feces of the accustomed female donor was significantly higher than on the control dish, as donors have consumed the cinnamon diet ($M_{duration} \pm SEM$; dish with feces: 66 ± 13 s, control dish: 18 ± 2 s, $n = 9$) ($p = 0.004$, Cohen's $d = 1.30$) or the cocoa diet ($M_{duration} \pm SEM$; dish with feces: 60 ± 2 s, control dish: 25 ± 2 s, $n = 7$) ($p = 0.02$, Cohen's $d = 1.83$).

Choice test Ten observers did not consume any diet during the choice test of 1 hr and were removed from the analysis of 1 hr test. However, after 24 hr of choice test, these same observers consumed at least one of the two diets and were thus reintegrated for the analysis of the 24 hr test.

During the choice test of 1 hr, males previously habituated to the feces of a female donor and having investigate the feces of the same female donor under cinnamon diet, consumed thereafter a higher proportion of cinnamon diet than males with a accustomed female donor under cocoa diet ($M_{proportion} \pm SEM$; cinnamon group: 0.63 ± 0.15, $n = 4$, cocoa group: 0.17 ± 0.07, $n = 6$), but the difference was not significant ($p = 0.12$, Cohen's $d = 1.13$) (figure 3.8A).

During the choice of test of 24 hr, however, males, previously habituated to the feces of the female donor and having investigate the feces of the same female

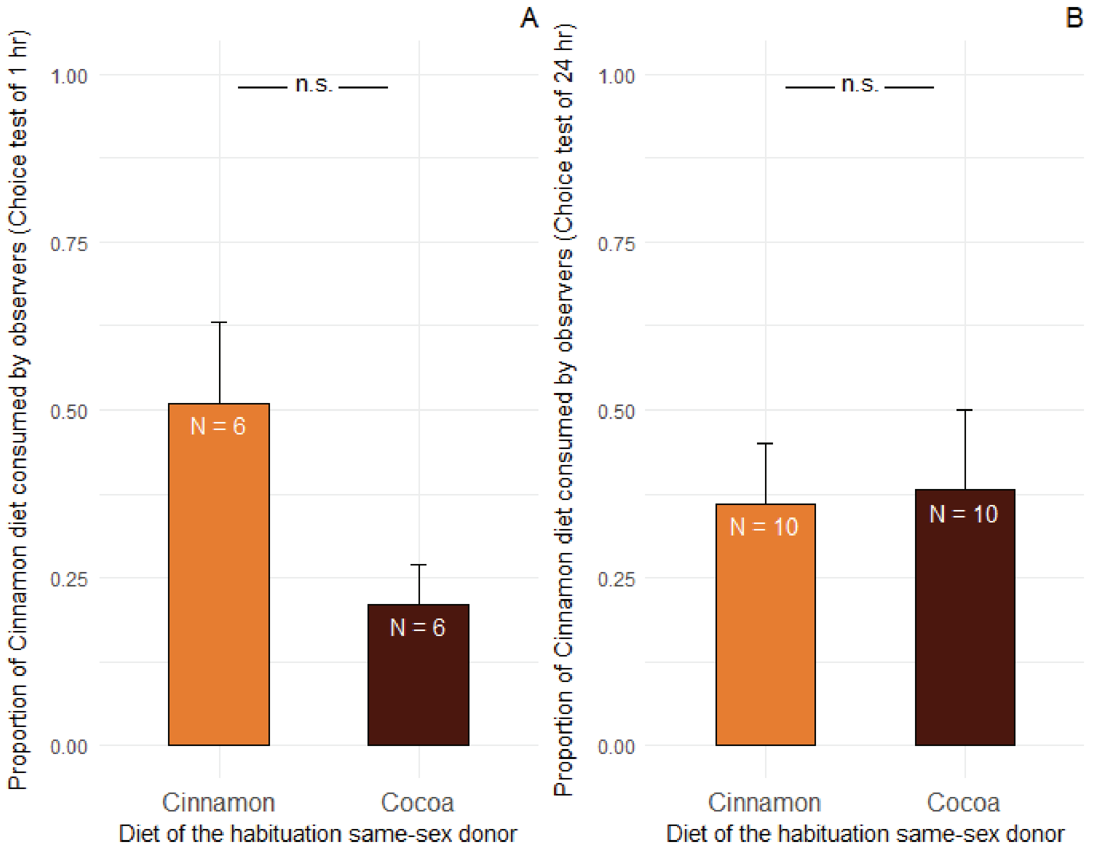

Figure 3.7 – Average proportion ($M + SEM$) of cinnamon diet consumed during a choice test of 1 hr (A) and of 24 hr (B) by male observers in each experimental group after the habituation to the feces of an unfamiliar male donor under cinnamon or cocoa diet. Comparisons by Fisher Pitman permutation tests for independent samples (n.s.: non-significant).

donor under cinnamon diet, ate significantly a higher proportion of cinnamon diet than males with a donor under cocoa diet ($M_{proportion} \pm SEM$; cinnamon group: 0.38 ± 0.11, $n = 10$, cocoa group: 0.05 ± 0.03, $n = 10$) ($p = 0.01$, Cohen's $d = 1.06$) (figure 3.8B).

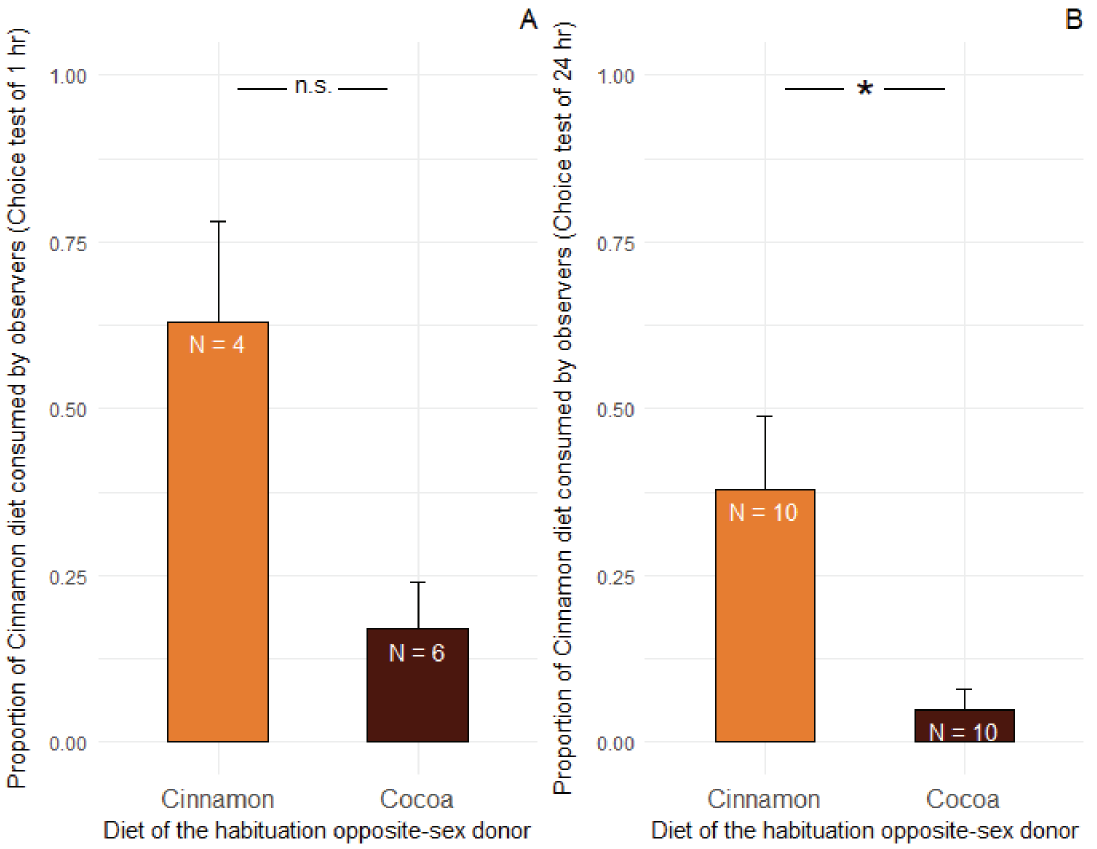

Figure 3.8 – Average proportion ($M + SEM$) of cinnamon diet consumed during a choice test of 1 hr (A) and of 24 hr (B) by male observers in each experimental group after the habituation to the feces of an unfamiliar female donor under cinnamon or cocoa diet. Comparisons by Fisher Pitman permutation tests for independent samples (*$p < 0.05$, n.s.: non-significant).

Experiment 4: effect of the presence of a competitor donor on the acquisition of indirect STFP

Social phase During the social phase, each observer was confronted with the simultaneous presence of the feces of two types of donors: an unfamiliar male and an unfamiliar female to which observers had been habituated.

Even in the presence of feces of an unfamiliar male donor, male observer spent significantly more time on the Petri dish containing the feces of the accustomed female donor than on the control dish, as donors have consumed the cinnamon diet ($M_{duration} \pm SEM$; dish with feces: 56 ± 8 s, control dish: 23 ± 2 s, $n = 9$) ($p = 0.008$, Cohen's $d = 1.33$) or the cocoa diet ($M_{duration} \pm SEM$; dish with feces: 54 ± 9 s, control dish: 18 ± 3 s, $n = 9$) ($p = 0.004$, Cohen's $d = 1.33$).

Male observers spent significantly less time on the Petri dish containing feces of the unfamiliar male donor after the introduction of the device with feces of the accustomed female donor than before, as donors have consumed the cinnamon diet ($M_{duration} \pm SEM$; before: 80 ± 6 s, after: 19 ± 3 s, $n = 9$) ($p = 0.004$, Cohen's $d = 1.77$) or the cocoa diet ($M_{duration} \pm SEM$; before: 56 ± 6 s, after: 15 ± 3 s, $n = 9$) ($p = 0.004$, Cohen's $d = 1.59$).

Choice test Five observers did not consume any diet during the choice test of 1 hr and were removed from the analysis of 1 hr test. However, after 24 hr of choice test, these same observers consumed at least one of the two diets and were thus reintegrated for the analysis of the 24 hr test.

During the choice test of 1 hr, after the presentation of feces of an unfamiliar male donor under standard diet, male observers, having investigate the feces of a accustomed female donor under cinnamon diet, did not consume a higher proportion of cinnamon diet than males with a accustomed female donor under cocoa diet ($M_{proportion} \pm SEM$; cinnamon group: 0.54 ± 0.09, $n = 8$, cocoa group: 0.33 ± 0.07, $n = 7$) ($p = 0.13$, Cohen's $d = 0.78$) (figure 3.9A).

Similarly, during the choice test of 24 hr, although all the ten animals of each group had consumed at least one of the two diets, the difference between the two experimental groups was not significant ($M_{proportion} \pm SEM$; cinnamon group: 0.38 ± 0.05, $n = 10$, cocoa group: 0.25 ± 0.07, $n = 10$) ($p = 0.17$, Cohen's $d = 0.64$) (figure 3.9B).

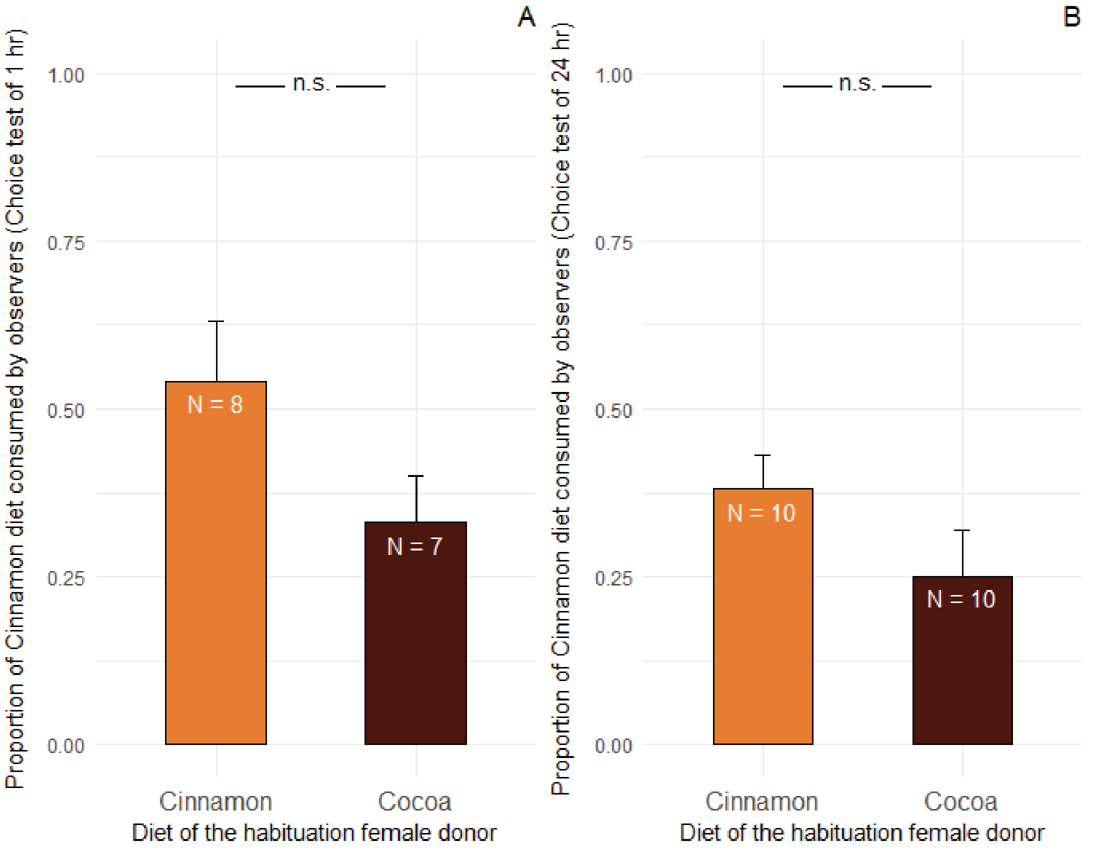

Figure 3.9 – Average proportion ($M + SEM$) of cinnamon diet consumed during a choice test of 1 hr (A) and of 24 hr (B) by male observers in each experimental group after the presentation of feces of an unfamiliar male donor under standard diet and of feces of an accustomed female donor under cinnamon or cocoa diet. Comparisons by Fisher Pitman permutation tests for independent samples (n.s.: non-significant).

Discussion

Our results revealed that in the context of the indirect social transmission of food preference (STFP), male and female house mice prioritize socio-olfactory information in different ways. Whatever the sex of the donor and its familiarity with the observer, female mice acquired an indirect STFP as shown in *Experiment 1* and *Experiment 2*. Under the same experimental conditions, house mouse males did not achieve an effective STFP when indirectly exposed to adult males, familiar or not and to unfamiliar females.

These results support the idea that, because food resources are a priority for females, they favor the food cues present in feces over the other cues characterizing the mouse donor. Indeed, this is consistent with the fact that in house mouse females, the reproductive success will be primarily influenced by their ability to rear the offspring after fertilization. Reproduction in small mammals is a very energetically demanding process and when there is not a sufficient quantity or quality of food the reproductive physiology and sexual behavior of females may be negatively impacted (Wade & Schneider, 1992; Wade & Jones, 2004; Schneider, 2004). Food-deprived female rodents usually suppress both ovulation and estrous behavior and food deprivation negatively impacts developing offspring when a gestation occurs (Wade & Schneider, 1992). Consequently, many aspects of the behavioral strategies of mammal females are profoundly influenced by these considerations (Ostfeld, 1990) and information about a new potential food source is of paramount importance for female mice. Our results also revealed that the characteristics of a potential sexual partner represented by an unfamiliar male donor did not interfere with the relevance of the food information perceived in feces. Access to sexual partners is one of the key elements of reproductive success but males do not constitute a limited resource for female house mice. Indeed, females of this species are tolerated and welcome by all adult males and therefore females have the opportunity to mate with different sexual partners throughout the year (Hurst, 1990c; Rolland et al., 2003). In the monogamous mound-building mouse, *Mus spicilegus*, an opposite result was observed during a habituation-discrimination task. Females investigating the body odor of an unfamiliar male were inclined to favor information relative to the characteristics of a potential sexual partner at the expense of information about a change in the diet of the donor (Colombelli-Négrel & Gouat, 2006). Mound-building mice and house mice are closed species but differ greatly in their socio-spatial organization. The paternal behavior displayed by mound-building mouse males contributes efficiently to the reproductive success of a female and mate selection is a key factor of female reproductive success (Patris & Baudoin, 2000; Gouat & Féron, 2005; Féron & Gouat, 2007).

Our results revealed that, contrary to females, males prioritized the information relative to a potential sexual partner, i.e. an unfamiliar female, rather than food-related information. A period of habituation to the odor of the unfamiliar female donor was nevertheless sufficient to induce an indirect STFP in males (*Experiment 3*) suggesting the novelty of the information relative to the female plays a key role in the selection of information. Under similar conditions, habituation to the odor of an unfamiliar male did not allow the clear establishment of an indirect STFP in males. These results are in agreement with those obtained in *Experiment 1* and suggest that, for males, the selection of information in the feces of another male is not dependent on the novelty of the information. In house mice, male reproductive strategies are directly related to territoriality (including overt conflict with other males) (Rowe & Redfern, 1969; Hurst, 1990a; Latham & Mason, 2004). The impairment of the indirect STFP between adult males may therefore be related to the fact that another adult male, familiar or not, is a potential competitor. This conclusion is supported by the results obtained when juvenile males served as donors. A juvenile male does not represent a threat for an adult male observer and even if information characterizing the juvenile was new, the indirect STFP was effective. The results obtained in *Experiment 4* confirmed the importance of information relative to a potential male competitor for adult males. The presence of an unfamiliar male's feces was sufficient to alter the acquisition of indirect STFP when the food information comes from a habituated female donor. Thus, the presence of information characterizing a potential competitor does not only alter the use of other information from this conspecific but seems to affect the general context of the acquisition of food information, even when it comes from another conspecific. Taken together, these results provide insight into the social environment perceived by mice and reveal the interest of indirect STFP in the study of these phenomena.

These differences of selection of information between males and females can have repercussions on the conditions of diffusion of food information within mouse populations. Actually females revealed to be the most open receivers as they are able to obtain information from a wide range of individuals. Moreover, they also appear to be kind of universal donor considering the STFP. On the other hand, adult males represent the less good mediators and probably obtain information on new food resources mainly through conspecifics (familiar females and juveniles) living on their territory. In other words, females appear to be potential keystones for the dissemination of food-related information inside a house mouse population.

Several studies highlighted the ability of rodents to detect in olfactory marks different information characterizing their conspecifics (Brown, 1979; Halpin, 1986). Olfactory marks constitute a unique source of different type of information that seems to be perceived relatively independently of each other (Colombelli-Négrel & Gouat, 2006; Raynaud, Messaoudi, & Gouat, 2012; Schellinck & Brown, 1999). Our study provides new elements into the use of these different types of information by mice and reveals the key role of individuals' concerns in the selection of information. Compared to other sensory systems, the olfactory system is the only one whose processing of information is not done directly at the level of the upper areas and is first treated by the olfactory bulb. Information provided by the olfactory bulb could have undergone modifications when it is transmitted to the upper areas (Cleland & Sethupathy, 2006; Shepherd et al., 2007). This could favor the competition between the different information present in olfactory marks and explained in part the selection of information. In addition, the olfactory bulb is regulated by cortical returns which can modulate its activity according to contingencies related to olfactory learning or the internal and external context (internal state of the animal, experimental conditions, environment) (reviewed by Rinberg & Gelperin, 2006). These elements could also play an important role in the selection of olfactory information. The mechanisms underlying the indirect STFP are to be explored but it is highly likely that attentional, motivational and emotional processes are involved in the processing and selection of socio-olfactory information. The indirect STFP offers excellent opportunities to determine how rodents process information about their socio-olfactory environment and how this can influence their behavior. It can also be a useful investigative tool for understanding information prioritization mechanisms within a single and composite stimulus.

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General discussion

Overview of results

Diversifying sources of supply is one of the key to an individual's survival and to its ability to adapt to changing environments. A species like the house mouse is able to colonize very different environments from its natural habitat of origin and is thus considered as a specialist of non-specialization (Morris, 1967). This ecological success implies drastic adaptations in its diet in order to make the optimal use of locally available resources. The objective of this thesis work was to determine how mice use their socio-olfactory environment to make food choices.

The socio-spatial organization of the house mouse expresses a certain diversity but is based essentially on the existence of territorial males structuring the social occupation of space (König & Lindholm, 2012). The male's strategy is to defend his territory towards other males while females prioritize access to resources to ensure their reproductive cycle and the survival of their young (Speakman, 2008). The direct encounter between two adult males systematically leads to violent conflict. Direct social transmission of food preference (STFP) is therefore probably excluded. The intolerance of females towards an unfamiliar female is less pronounced than intolerance between males (Patris et al., 2002). We have shown, however, that even in the absence of agonistic behavior, direct STFP was not functional between unfamiliar females. Our results revealed, nevertheless, that this direct STFP is fully functional between familiar females. Under similar conditions, indirect STFP, which allows the transfer of information without the need for direct contact between conspecifics, has been found to be more effective by allowing both a transfer of food information between familiar and between unfamiliar females. The efficiency of indirect STFP between unfamiliar females suggests that the alteration of direct STFP is not a consequence of the origin of social information (a potential competitor) but seems more affected by the social context induced by the interaction between the conspecifics. These results raise questions about the processes that could affect the acquisition of this social learning and suggest in particular the implication of emotional processes. They also reveal that, unlike social interactions, olfactory marks of unknown conspecifics appear to be less costly for mice to access information on new food resources.

Our results also revealed that indirect STFP presents significant physical constraints that may impact the acquisition conditions of food information. In our first experiments on indirect STFP, we had successfully used two different diets (artificial paste and oat grains). The proposed diets thus differed in a large number of odorant molecules creating as many possibilities of pairing between the olfactory marks and the new food item. We then studied whether the diversity of olfactory markers characterizing the diet played a key role in identifying the food odor present in the feces. The behavioral study was systematically doubled by a biochemical study by gas-chromatography coupled with mass-spectrometry (GC-MS) to determine the presence of odorant molecules in biological media. We have shown, in the context of indirect STFP, that a single odorant molecule was not effective because it disappeared during digestion. To answer this problem, we used a system of protection of the odorant molecule during intestinal transit. We showed by analysis in GC-MS that the protected molecule was found in the feces of the donors. Nevertheless, and contrary to what was observed in direct STFP, indirect STFP was not functional, suggesting that different perceptual processes are involved in these two learning pathways.

We then developed a mixture of odorant molecules, mimicking them by simplifying certain essential oils (Damascus rose essential oil and clove essential oil). This mixture coupled with the protection and included in the paste diet proved effective allowing the indirect STFP. All of these data show that the multiplicity of olfactory markers characterizing the diet, not only reduces the constraints associated with the molecules degradation during digestion but also seems to be a necessary condition for the detection of the food source in the feces. The reasons for such difference in treatment between direct and indirect transmission still raise questions about the underlying neurobiological processes related to perception of olfactory information and are yet to be explored.

Finally, although we have shown that indirect STFP can reduce the constraints associated with the presence of a conspecific, the different type of information characterizing the donor and present in feces can interfere with information about a new food resource and thus affect the acquisition of indirect STFP. We have shown that females can, in addition to feces of familiar and unfamiliar females, take into account food information from the feces of an unfamiliar male. However, males are much more resistant. Faced with the odors of an unfamiliar female, they can only consider information about their diet after a period of habituation with their olfactory marks. With respect to a familiar and an unfamiliar male, and even after a period of habituation, indirect STFP was not demonstrated. The characteristic of potential competitor seems to be at the origin of the impairment because indirect STFP is possible when the donor is a juvenile male. Our results also revealed that in the presence of a competitor's feces, food information from another non-competing conspecific is not used by males. This suggests that the characteristic of a potential competitor does not only alter the acquisition of information from the competing donor but also induces a general context in which males are unable to use other information, including that from another source. We suggest that these results in male and female mice are strongly related to a selection of information during the investigation of the feces of a conspecific, dependent on the concerns of the individuals and that can be related to the strategies of reproduction of each sex.

Consequently, all of these results allowed us to have a broader view of the conditions under which STFP can be functional in the house mouse, *Mus musculus domesticus*. Our results suggested the involvement of different brain mechanisms in the processing of socio-olfactory information allowing the acquisition of this social learning.

Anxiety and memory processes

Circumstances in which animals perceive information are known to affect critically key aspects of learning and memory processes (Holland & Bouton, 1999; Maren & Holt, 2000; Matsumoto & Mizunami, 2004). Among such circumstances, the social context may play an important role, especially in social learning. According to classical appetitive conditioning, social learning would take place when social context involves positive and rewarding states whereas non-rewarding social contexts would produce less or no learning (Choleris et al., 2011). In the context of the direct social transmission of food preference (STFP), the nature of the interaction plays a major role in its acquisition. Our results revealed that contrary to encounters between familiar female house mice, interaction between unfamiliar females produces an agonistic social context which alter the transfer of food information between individuals. This agonistic social context affects the behavior of the observer (e.g. investigative behavior) but also probably its emotional state. Indeed, results of investigations with mice have shown that agonistic interactions are associated with social stress and an accompanying enhancement of anxiety and anxiety-related behavior (Galef & Wigmore, 1983; Avgustinovich, Gorbach, & Kudryavtseva, 1997).

The olfactory sense is known to have a unique relation with emotion and memory. Unlike other senses, the olfactory system interfaces with primary emotional areas such as the amygdala, hippocampus and orbitofrontal cortex, via extensive reciprocal axonal connections (Carmichael et al., 1994; Haberly, 2001; Gottfried, 2010). These three areas are also involved in some type of learning and memory processes. The orbitofrontal cortex receives strong olfactory inputs from the piriform cortex and medial thalamus and is important for olfactory learning and memory (Petrulis & Eichenbaum, 2003). The orbitofrontal cortex is also reciprocally connected with the medial temporal lobe, including the perirhinal and entorhinal cortices (Deacon, Eichenbaum, Rosenberg, & Eckmann, 1983; Barbas, 2000), which play a key role in learning and memory processes (reviewed by Eichenbaum, 2000). The hippocampus is involved in the selection and transmission of information in working memory, short- and long-term memory transfer, and various declarative memory functions (reviewed by Eichenbaum, 2004). The amygdala, for its part, may mediate the rapid acquisition of behaviors based on biologically significant events with affective properties (White & McDonald, 1993). It also participates in olfactory and taste associative learning (Wang, Fontanini, & Katz, 2006). Consequently, the contribution of these different brain areas involved in olfactory perception and in both emotional and memory mechanisms, raises the possibility that emotional processes may influence social learning and contributes to the impairment of the STFP between unfamiliar mice.

In addition to being an ethologically based social behavior, the STFP paradigm has been extensively used in rodents as a test of olfactory memory. STFP is particularly mechanistically interesting for neurobiologists because it exploits an animal's ability to learn quickly and to remember information about social olfactory cues (Galef & Wigmore, 1983; Strupp & Levitsky, 1984; Lesburguères et al., 2011). In addition, the STFP offers characteristics that belong to declarative or relational memory (Bunsey & Eichenbaum, 1995; Alvarez et al., 2001; Lesburguères et al., 2011). Thus, thanks to the interest of neurobiologists for the STFP, several studies made it possible to reveal brain regions involved in the acquisition, storage and retrieval of the STFP task. Among those, it was suggested that the hippocampus plays a key role in the consolidation of the STFP but not in its acquisition or short-term retention (Bunsey & Eichenbaum, 1995). As a result, it is unlikely that the hippocampus is involved in the alteration processes observed in our experiments. In another study, it was showed that the cholinergic projections to the orbitofrontal cortex are likely to be pivotal in the acquisition of food preference (Ross, McGaughy, & Eichenbaum, 2005). It was also suggested that the prelimbic cortex is important for the acquisition and early consolidation of the STFP task (Carballo-Márquez et al., 2007). Finally, although information in the literature regarding the role of the amygdala is not completely clear, it was suggested that the amygdala is involved in acquisition and memory formation of STFP (Boix-Trelis, Vale-Martínez, Guillazo-Blanch, Costa-Miserachs, & Martí-Nicolovius, 2006; Vale-Martínez, Baxter, & Eichenbaum, 2002). As a result, the amygdala and the orbitofrontal cortex seem to be key structures in STFP acquisition and in its connection to emotions.

Several studies indicate that the emotional status of rodents can affect the memorization of social information (reviewed by van der Kooij & Sandi, 2012). These observations are in agreement with an important body of data showing, from a general point of view, that emotional experiences, including stress, can affect the formation of memory (reviewed by van der Kooij & Sandi, 2012). For example, anxiety has been shown to affect performance of a number of laboratory spatial learning tasks, including the Morris water maze and radial maze (Perrot-Sinal, Heale, Ossenkopp, & Kavaliers, 1996; Shors & Dryver, 1992). However, although the modulation of social memory formation by acute stress has been investigated in the social recognition task and social hierarchy formation, no information is available as to whether stress might affect an individual's capability to form memories when learning from others. Our results, interpreted in the context of the social constraints of the house mouse, suggest that socially induced anxiety could alter the acquisition of the direct STFP. This social constraint has not been demonstrated in first generation laboratory bred wild rats as well as domesticated rats (Galef et al, 1984) and laboratory mice (Valsecchi1994). Although previous studies on other less tolerant species exist (e.g. Valsecchi et al, 1996), our results offer novelty on this topic by providing a comparison between direct and indirect STFP. Indeed, the absence of the conspecific during the indirect STFP removes this physical constraint and provides a different social context that allows the acquisition of STFP, supporting the idea that the nature of the social interaction play a key role in the alteration of the direct STFP. These results offer a panel of research to work on this topic and to study the mechanisms involved in the alteration of STFP in a stressful context.

Selective attention modulates sensory processing

Multisensory perception

Most studies on perception consider each sense — vision, hearing, touch, olfaction and so on — independently, as if each sensory modality was an entirely separate module. In many situations, however, our different senses receive correlated information about the same external objects or events, and this information is combined in our brains to yield multisensory determined percepts (Driver & Spence, 2000). Specific events from the outside world often stimulate several of our senses simultaneously, as it is the case when two individuals interact together. For example, in humans, watching lip-movements can alter which phoneme is heard for a particular sound (McGurk & MacDonald, 1976). In this case, different modalities can provide convergent information about the same external event or property.

Several studies showed that interactions between olfactory and other sensory modalities may contribute to effective odor perception (Zellner & Kautz, 1990; Dalton, Doolittle, & Nagata, 2000; Distel & Hudson, 2001). For example, Gottfried and Dolan (2003) highlighted that the olfactory perception in humans can be strongly influenced by visual cues. In this study, subjects participated in an olfactory detection test, in which odors and images were delivered together or separately. The authors demonstrated the facilitation of odor detection when congruent visual cues were presented at the same time. Although the multimodal integration which is mediated in the brain is not completely understood, animal studies indicate that various anatomical sites receive convergent inputs from different sensory modalities. It is the case for the hippocampus that receive direct and indirect inputs from different sensory modalities (Deadwyler, Foster, & Hampson, 1987; Small, 2002). Another site that may participate in multimodal integration is the orbitofrontal cortex. This structure is the principal neocortical element of the olfactory system, and it has a pivotal associative role in olfactory information processing (Gottfried & Zald, 2005; Schoenbaum & Eichenbaum, 1995) and higher-order multimodal integration (Li et al., 2010). The facilitation of odor detection when congruent visual cues were present has been associated with enhanced neural activity in these two brain areas (Gottfried & Dolan, 2003).

As mentioned previously, the orbitofrontal cortex and the hippocampus represent two brain structures that have been shown to play a key role in the acquisition of the social transmission of food preference (STFP). Thus, taking into account these elements, it is possible that other sensory modalities influence the detection of olfactory information required for the STFP. During the direct STFP, the observer has access to olfactory information from the demonstrator (including information about food sources consumed) but also to different sensory information dependent on their social interaction. Indeed, the social interaction or even mere presence of the conspecific gives additional information to the observer. In this case, many visual, tactile and auditory information will also characterize the interaction. During the indirect STFP, information characterizing the conspecific is purely of olfactory nature. The modulation of olfactory perception could therefore be different between direct and indirect STFP.

The brain uses different mechanisms that allow it to adapt flexibly to the environment. These include mechanisms that guide sensory processing and the resolution of competing choices. These abilities are usually attributed to selective attention and executive functions that allow the brain to process a subset of information in the environment based on its relevance (Vuilleumier, 2005). Refined perception significantly builds on such selective attention in decision-making processes and, in turn, is deeply context-dependent in its nature. Many authors have highlighted links between multimodal processes and attention. For example, the presentation of any stimulus can automatically direct attention to its source of emission (exogenous attention) and facilitate the processing of a second stimulus of different modality having the same spatial source and presented in the same time period (Eimer, 2001; Spence, 2002).

An element that we highlighted from our studies is that, contrary to indirect STFP, direct STFP between female house mice was clearly established when the information support was a single odorant compound. During the direct STFP, the presence of a conspecific could, therefore, focus attention to information characterizing it and thus facilitate the detection of food information necessary for the acquisition of the STFP. A central prediction arising from studies of multisensory integration states that multimodality should enable an individual to improve the detection of information, particularly when a stimulus in one modality is ambiguous or underdetermined (Stein & Meredith, 1993). This could explain why these differences between direct and indirect STFP are observed when the food information is reduced to a single odorant compound. Thus, our results open up a possible way of research in the field of multisensory brain processes. Further studies would however be necessary to explore the underlying mechanisms allowing the processing of information necessary for the acquisition of the direct and indirect STFP.

Simultaneous perception of different types of information from the same olfactory source

Mice and other mammals use olfactory marks in a number of social, agonistic, and defensive contexts. These odors convey information about other animals including species, sex, and individual identity (Bowers & Alexander, 1967; Halpin, 1986; Hurst et al., 2001). They constitute relevant sources of information about traits of individuals as well as metabolic information such as reproductive, health and nutritional status (Kavaliers, Colwell, & Choleris, 2005; Osada et al., 2003; Barnard & Fitzsimons, 1988; Mossman & Drickamer, 1996). Several studies demonstrated that rodents were able to discriminate the modifications of olfactory marks induced by diet factors (Colombelli-Négrel & Gouat, 2006; Ferkin et al., 1997; Raynaud et al., 2012). Colombelli-Négrel and Gouat (2006) demonstrated, using a habituation-discrimination procedure, that mound-building mice, *Mus spicilegus*, were able to keep track of the identity of the donor despite a change of diet. It was suggested that identity and diet information were detected as independent odor cues. Such a conclusion about the independence of traits and states of donors was also drawn from studies performed in laboratory rodents (Brown et al., 1996; Kwak et al., 2008). These studies have greatly contributed to understanding how socio-olfactory information can be perceived by rodents. However, although these commonly used procedures allow to assess the ability of rodents to detect information, they do not allow to establish in which social context individuals use this information. Indirect STFP brings a novelty to the study of social odors insofar as it makes it possible to evaluate the use of socio-olfactory information by individuals. The differences observed between males and females in the *Chapter 3* of this manuscript have revealed the value of this paradigm. Indeed, an essential point that we have shown, is that although an individual may be able to detect a type of information in the olfactory marks of a conspecific, the use of this type of information requires the involvement of more complex underlying mechanisms such as prioritization and selection of information, depending on the needs and concerns of the individual.

In the context of indirect STFP, it appears that mice can perceive in the feces of their conspecifics both social information characterizing the donor and information about its diet. Our results suggest that, in males, a competition between social and diet information during the investigation of these olfactory marks can affect the acquisition of the indirect STFP. Compared to other sensory systems, the olfactory system is the only one whose processing of information is not done directly at the level of the upper areas and is first treated by the olfactory bulb. In the olfactory bulb, the activities of mitral and tufted cells are regulated by an interneuron circuit (juxtaglomerular cells and granular cells) that allows communication within and between glomeruli (Cleland & Sethupathy, 2006; Shepherd et al., 2007). They participate in the processes of self-inhibition of the less activated glomeruli and of interglomerular inhibition, making it possible to increase the signal-to-noise ratio of the sensory message. The consequence of this organization is that information provided by the olfactory bulb could have undergone modifications when it is transmitted to the upper areas. This could favor the competition between the different information present in olfactory marks and explained in part the selection of information. In addition, the olfactory bulb is regulated by cortical returns which can modulate its activity according to contingencies related to olfactory learning or the internal and external context (internal state of the animal, experimental conditions, environment) (reviewed by Rinberg & Gelperin, 2006). These elements could also play an important role in the selection of olfactory information.

For mice, odorant stimuli are the primary means of motivating almost every aspect of their behavior. Maternal bonding, kinship recognition, food search, mate selection, predator avoidance, and territorial marking are all guided by smells. Sometimes, individuals can be confronted with classes of stimuli that have more direct relevance for their well-being and survival than others. For instance, some stimuli may signal danger or threat, such as predators or enemies, whereas other stimuli signal chances for growing and expansion, such as potential mates or food sources. Such stimuli require rapid adaptive responses, such as evading the threat or approaching the positive stimulus. One might expect that, given the high importance of such valenced stimuli for the organism, the perceptual processing of these stimuli should be prioritized to allow for a rapid appraisal of the situation and consequently the rapid preparation of an appropriate behavioral response. The selection of information for the establishment of appropriate behavior could then depend on emotional and attentional processes mediated by neurally organized defensive and appetitive motivational systems.

The orbitofrontal cortex is known to play a key role in motivated behavior. It has been shown to contain a representation of various natural reinforcers, both appetitive and aversive, and to be involved in encoding the subjective value of stimuli (Azzi, Sirigu, & Duhamel, 2012). Orbitofrontal cortex is heavily involved in circuits related to olfactory processing as well as limbic structures such as the amygdala (Kolb, 1984). This structure is also part of a network of structures involved in adaptive behavior and decision making. According to the results of their study in the rat, Schoenbaum, Chiba, and Gallagher (1999) suggested that basolateral amygdala could be involved in the encoding of the motivational significance of cues whereas orbitofrontal cortex uses this information in the selection and execution of an appropriate behavioral strategy. By the same token, reciprocal connections may allow processing in orbitofrontal cortex to regulate networks in basolateral amygdala. Thus, these two regions would function cooperatively, along with other interconnected structures, in the production of goal-directed behavior that reflects the motivational significance of cues. The involvement of these two brain structures in the acquisition of the STFP reveals them to be good candidates to study the mechanisms underlying this selection of information during indirect STFP. Viewed from this perspective, the indirect STFP provides a potentially useful model for the study of neurobiological mechanisms underlying the selection of socio-olfactory information in rodents.

Consequences for natural populations

The overall results of this thesis work brings a broader vision conditions in which social transmission of food preference (STFP) could be used by house mice. Indeed, taken together, these results reveal the importance of the social context, in which information is perceived by mice, to determine the use of social cues during their food choices. As we predicted, the social organization of the house mouse and the social constraints associated with it play a key role in socially enabling the transmission of information about new food sources.

If unfamiliar individuals regularly avoid themselves and interact only in the context of defense territory, it seems difficult to exchange food information in these conditions. We have assumed that the impairment observed during direct STFP between unfamiliar females was probably due to the stressful social context that disrupts the learning and memory processes necessary for the acquisition of the STFP. Following this hypothesis, encounters between two unfamiliar males being more aggressive than those between females (Patris et al., 2002), direct STFP between unfamiliar mice of same-sex should be generally precluded. The assessment of direct STFP in house mice of wild origin between unfamiliar individuals of the opposite sex has, to my knowledge, never been studied. In natural conditions, male mice are particularly intolerant of other male intruders whereas male-female interactions between unfamiliar conspecifics are generally characterized by a low frequency of agonistic behavior (Bronson, 1979; Crowcroft & Rowe, 1963; Palanza et al., 1996). It is then possible that the interaction between a male and a female mice may allow the establishment of a direct STFP as is the case between familiar individuals. However, we have seen in the context of the indirect STFP, that despite the absence of direct interaction, information characterizing an unfamiliar female can overshadow food information and impair the acquisition of the STFP in males. These elements could also affect males as part of the direct STFP. Recently, Andrade (2017) provided results on direct STFP in the Algerian mouse of wild origin, *Mus spretus*. She highlighted that interactions between unfamiliar male and female conspecifics allow a clear direct STFP, whatever the sex of the observer. These results suggest that information characterizing an individual of the opposite sex does not appear to alter the acquisition of direct STFP. This is consistent with the idea that olfactory information can be modulated differently between direct and indirect STFP. However, it is important to note that the socio-spatial organisation differs greatly between *Mus spretus* and *Mus musculus domesticus*, making comparison more difficult to establish (Cassaing & Croset, 1985). In *Mus spretus*, a behavior of social attachment was observed between usual mates whereas *Mus musculus domesticus* males were friendlier towards an unknown female than their own mate (Cassaing & Isaac, 2007). In the house mouse, it is difficult to establish a general pattern resulting from interactions between individuals of opposite sex. It is therefore very likely that the transmission of information on new food sources between individuals of different sex may be possible but strongly depends on the nature of their encounter. Overall, these data suggest that, although in some cases the direct STFP could be established between unfamiliar individuals, in general, in wild house mice populations direct STFP should be limited to familiar individuals, i.e. females and males living on the same territory (König & Lindholm, 2012).

Yet, as it has been mentioned above, the interest of mice in learning from unfamiliar conspecifics is great because their food repertoire varies more than within a social group. Many studies have revealed the predominant role of olfactory marks in olfactory communication of house mice (Hurst, 1990a, 1990b, 1990c) but so far, few studies have focused on their role in the food strategies of this species. This thesis work revealed the major importance of olfactory marks on food choice in mice. Because it does not require the presence of the conspecific, indirect STFP seems to be a good way to obtain information from unfamiliar conspecifics, which would then widen the range of potential feeding items in natural conditions. If blocking points, especially in males, persist in the context of indirect STFP, our results suggest that the dissemination of information on a new food ressource is possible within a population, in particular through females. Indirectly, they can use information from any type of conspecifics and represent the mediators best accepted by all of the different types of individuals in the population (figure 3.10). The information carried by a female could subsequently spread within its social group via the two STFP ways, thus allowing males to also acquire information about new food resources.

Thus, direct and indirect STFP appears to be complementary under natural conditions, each extending the conditions for the transmission of food information in rodents. Studies realized in natural conditions on wild populations could be used to translate these results to a population level, thus allowing to better understand the food strategies developed by mice.

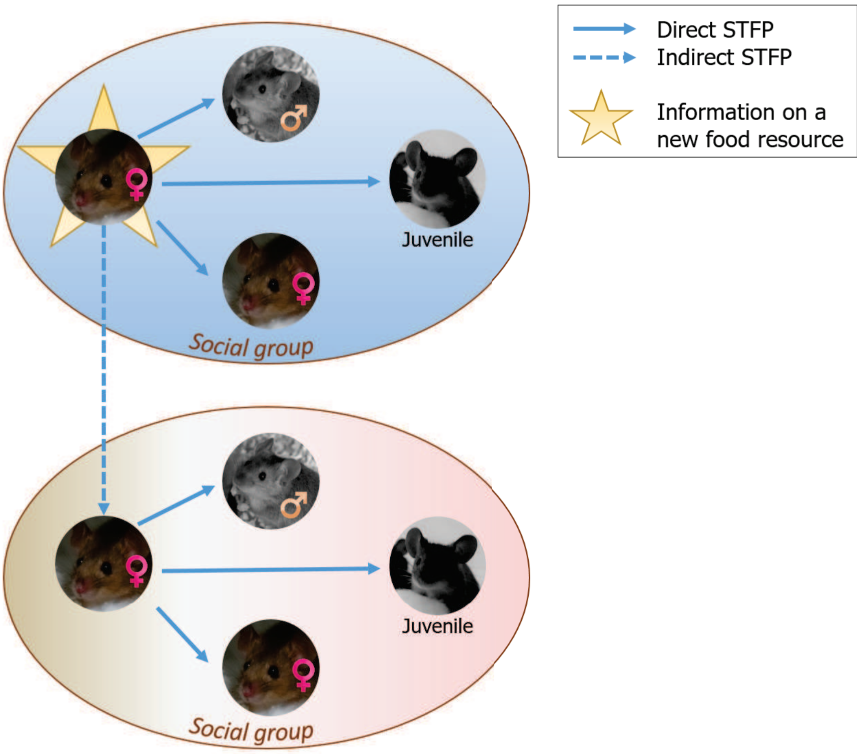

Figure 3.10 – Possible dissemination of information on a new food ressource in population of house mice, *Mus musculus domesticus*

Bibliography of the current chapter

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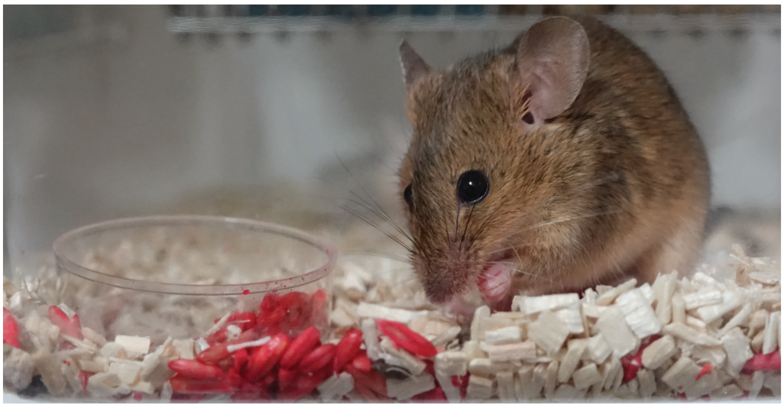
Appendix

Evaluation of the spontaneous consumption by mice of the diets used



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Objective

The diets presented during the procedure of choice test may have different attractiveness for mice depending on their composition. In addition to social information, these differences in attractiveness could play a role in food consumption of individuals. The idea is therefore to evaluate if the different diets used in our experiments present significant consumption variations in mice during a spontaneous presentation of the diet.

Method

The origin of the animals and the general procedures used are the same as those described in the chapters of the manuscript. The tests, for each pair of diets used in a choice test, were performed in a random order on 7 female subjects.

When the social transmission of food preference (STFP) was also tested in males (i.e. with cocoa and cinnamon diets), 7 additional males were tested. For each pair of diets whose composition differs only by the addition of an odorant, the consumption of the basic diet (i.e. the artificial paste) was also evaluated. Each subject passes the test individually. Simultaneously with the standard diet, a 3 g sample of the diet tested was placed in a Petri dish to limit the dispersion of unconsumed food and placed inside the home cage of the subject. Depending on the duration of the experiments conducted to study the STFP, the subject's consumption was noted at 10 min, 1 hr and 24 hr. A 24-hr break will be made between each test for the same subject.

Analysis

Because of the small number of animals in each group ($N < 30$), we used non parametric statistics. The results were significant when $p \leq 0.050$. In order to compare consumption between different diets, we used Fisher Pitman permutation tests for paired samples with an approximation of 100,000 by the Monte-Carlo method.

Results

Paste and oat diets

During the consumption test of 10 min, the amounts of oat and paste diets consumed were very low and female subjects did not consume them differently ($M_{consumption} \pm SEM$; oat diet: 0.03 ± 0.02, paste diet: 0.15 ± 0.10, $n = 7$)($p = 0.50$).

Cinnamaldehyde and eugenol diets

When single odorant molecule was added to the paste diet, female subjects did not consume differently the cinnamaldehyde diet and the eugenol diet compared to the paste diet during the consumption test of 10 min ($M_{consumption} \pm SEM$; paste diet: 0.13 ± 0.03, cinnamaldehyde diet: 0.12 ± 0.03, eugenol diet: 0.12 ± 0.02, $n = 7$)($p = 0.98$, figure 11A).

Similar results were obtained during the test of 1 hr ($M_{consumption} \pm SEM$; paste diet: 0.36 ± 0.05, cinnamaldehyde diet: 0.34 ± 0.08, eugenol diet: 0.38 ± 0.05, $n = 7$)($p = 0.84$, figure 11B).

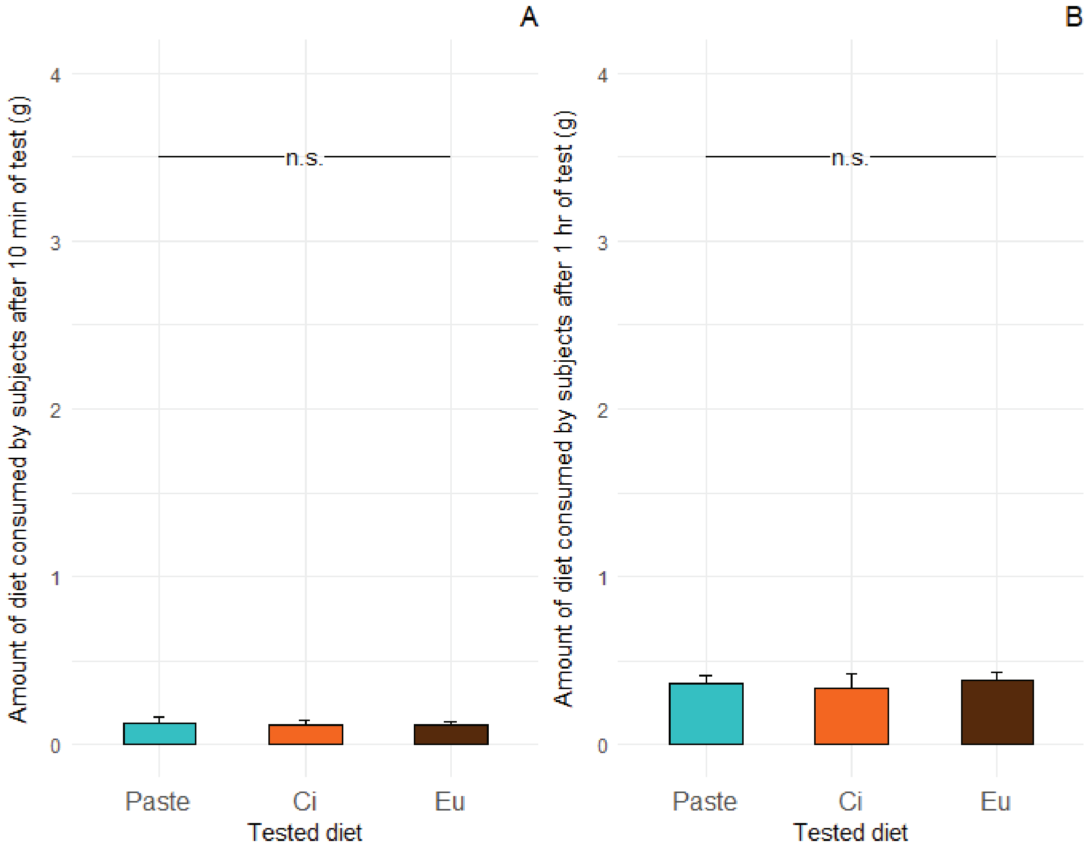

Figure 11 – Average amount ($M + SEM$) over 3 g of paste, cinnamaldehyde and eugenol diets consumed by female subjects ($n = 7$) during a consumption test of 10 min (A) and of 1 hr (B). Comparisons by Fisher Pitman permutation tests for paired samples (n.s.: non-significant).

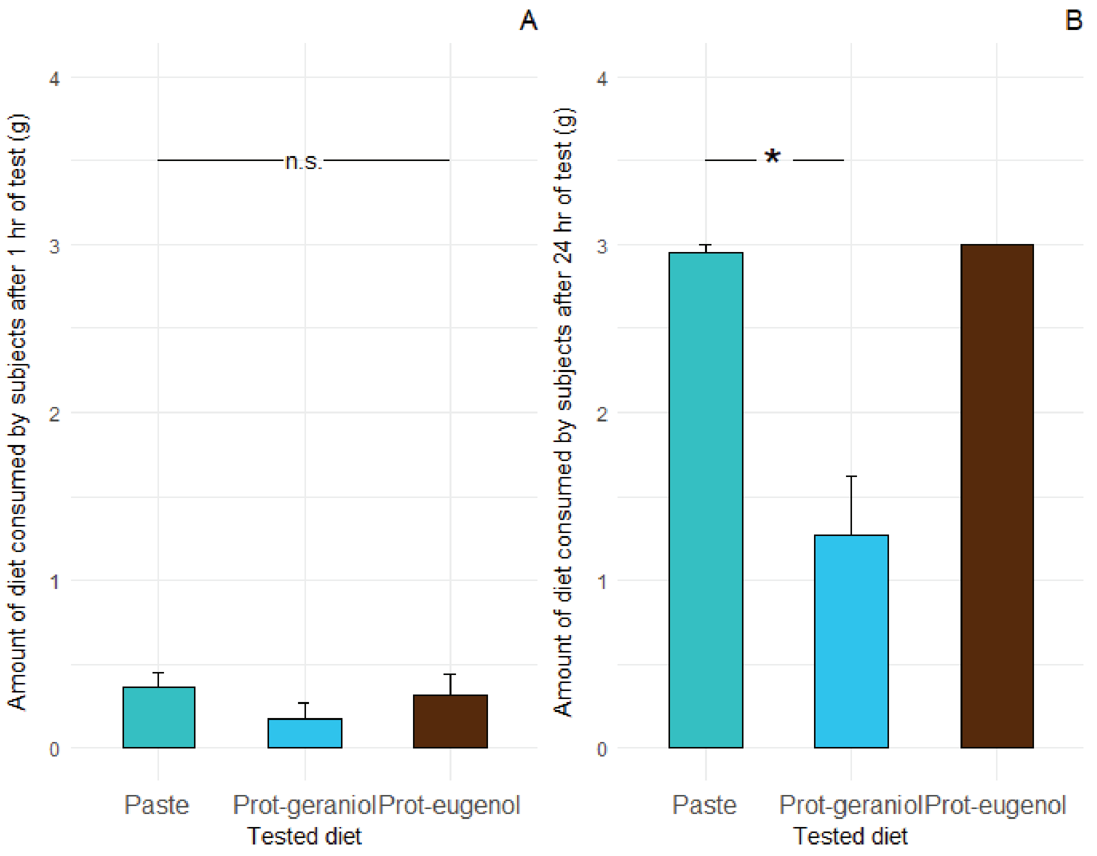

Figure 12 – Average amount ($M + SEM$) over 3 g of paste, protected-geraniol diet and protected-eugenol diets consumed by female subjects ($n = 7$) during a consumption test of 1 hr (A) and of 24 hr (B). Comparisons by Fisher Pitman permutation tests for paired samples (n.s.: non-significant, $^*p < 0.050$).

Protected-geraniol and protected-eugenol diets

During the consumption test of 1 hr, female subjects did not consume differently the protected-geraniol and protected-eugenol diets compared to the paste diet ($M_{consumption} \pm SEM$; paste diet: 0.36 ± 0.09, protected-geraniol diet: 0.17 ± 0.10, protected-eugenol diet: 0.32 ± 0.12, $n = 7$)($p = 0.86$, figure 12A).

However, during the test of 24 hr, unlike the protected-eugenol diet which is entirely consumed by all subjects, females consumed significantly less the protected-geraniol diet compared to the paste diet ($M_{consumption} \pm SEM$; paste diet: 2.95 ± 0.05, protected-geraniol diet: 1.27 ± 0.35, protected-eugenol diet: 3.00 ± 0.00, $n = 7$)($p = 0.03$, figure 12B).

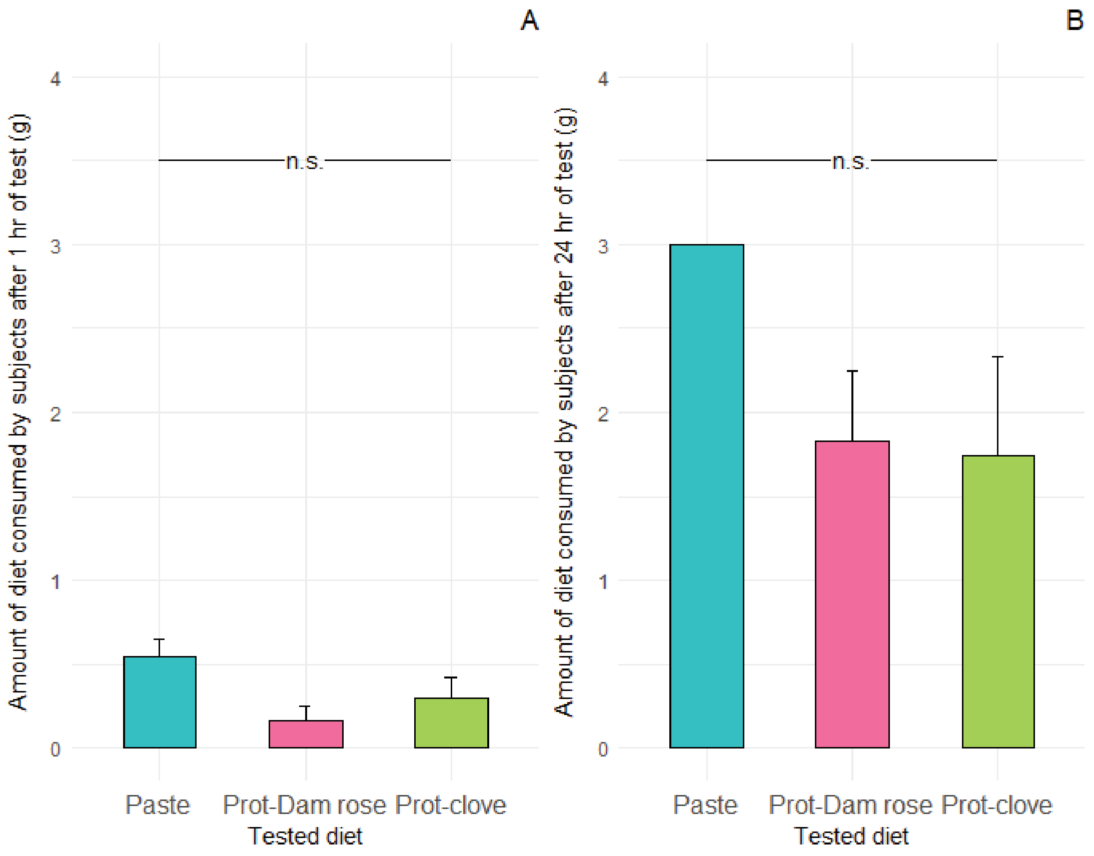

Figure 13 – Average amount ($M + SEM$) over 3 g of paste, protected-Damascus rose and protected-clove diets consumed by female subjects ($n = 7$) during a consumption test of 1 hr (A) and 24 hr (B). Comparisons by Fisher Pitman permutation tests for paired samples (n.s.: non-significant).

Protected-Damascus rose and protected-clove diets

During the consumption test of 1 hr, female subjects did not consume differently the protected-Damascus rose diet and the protected-clove diet compared to the paste diet ($M_{consumption} \pm SEM$; paste diet: 0.54 ± 0.11, protected-Damascus rose diet: 0.16 ± 0.09, protected-clove diet: 0.30 ± 0.12, $n = 7$)($p = 0.38$, figure 13A).

However, during the test of 24 hr, although the difference was not significant, the consumption of the protected-Damascus rose diet and the protected-Clove diet were reduced compared to that of the paste diet ($M_{consumption} \pm SEM$; paste diet: 3.00 ± 0.00, protected-Damascus rose diet: 1.83 ± 0.42, protected-clove diet: 1.74 ± 0.59, $n = 7$)($p = 0.09$, figure 13B).

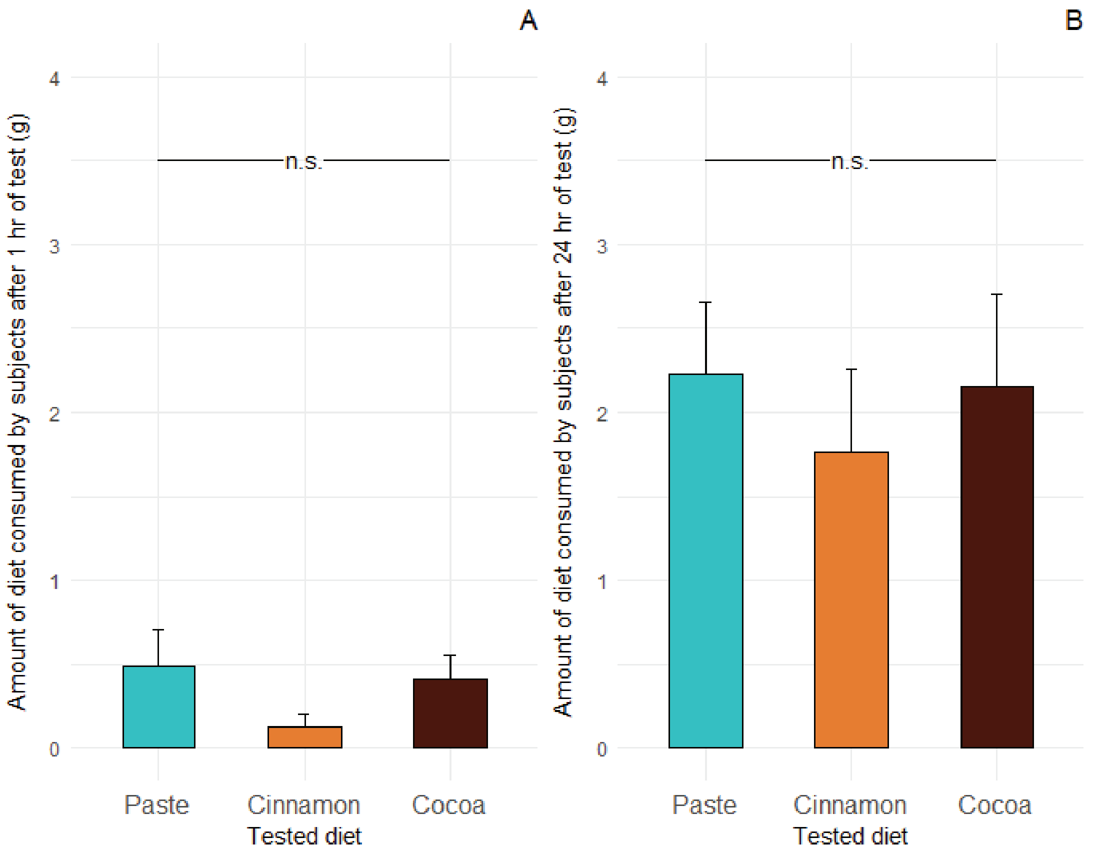

Figure 14 – Average amount ($M + SEM$) over 3 g of paste, cinnamon and cocoa diets consumed by female subjects ($n = 7$) during a consumption test of 1 hr (A) and of 24 hr (B). Comparisons by Fisher Pitman permutation tests for paired samples (n.s.: non-significant).

Cinnamon and cocoa diets

Females When food additive was added to the paste diet, female subjects did not consume differently the cinnamon diet and the cocoa diet compared to the paste diet during the consumption test of 1 hr ($M_{consumption} \pm SEM$; paste diet: 0.49 ± 0.22, cinnamon diet: 0.13 ± 0.07, cocoa diet: 0.41 ± 0.14, $n = 7$)($p = 0.53$, figure 14A).

Similar results were obtained during the test of 24 hr ($M_{consumption} \pm SEM$; paste diet: 2.23 ± 0.43, cinnamon diet: 1.76 ± 0.50, cocoa diet: 2.15 ± 0.55, $n = 7$)($p = 1$, figure 14B).

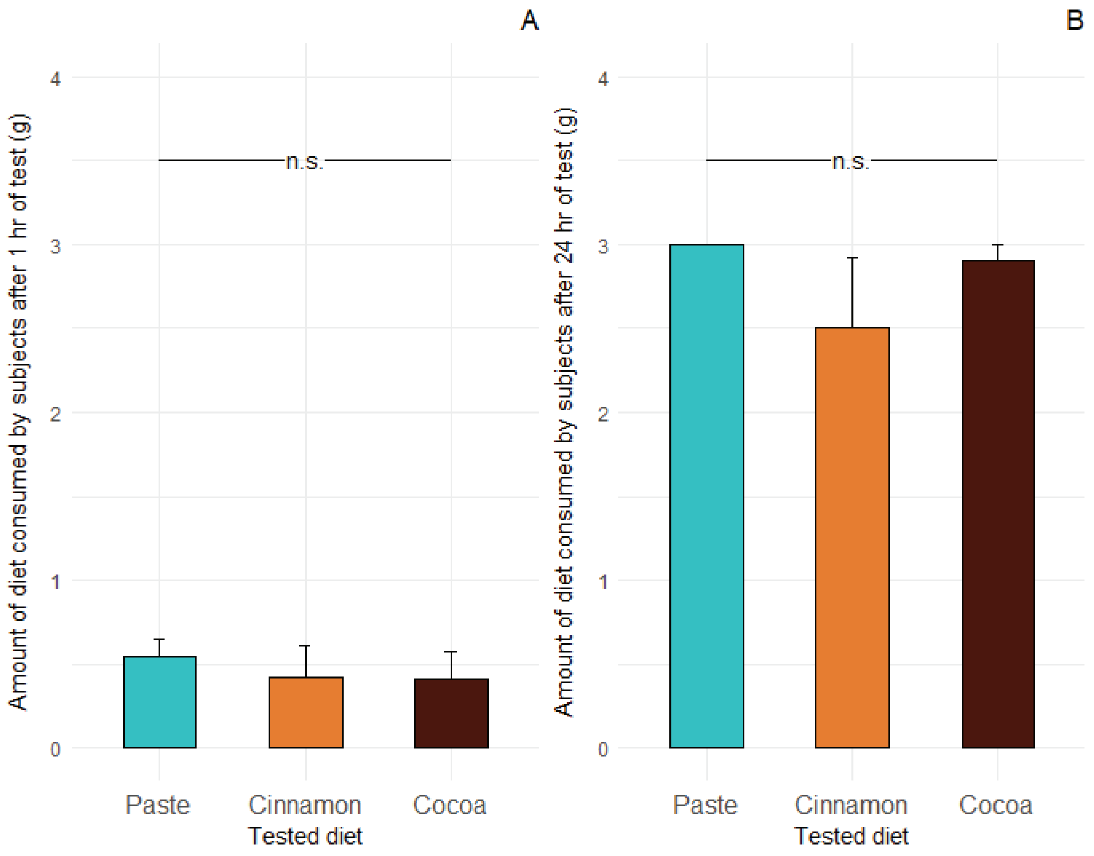

Figure 15 – Average amount ($M + SEM$) over 3 g of paste, cinnamon and cocoa diets consumed by male subjects ($n = 7$) during a consumption test of 1 hr (A) and of 24 hr (B). Comparisons by Fisher Pitman permutation tests for paired samples (n.s.: non-significant).

Males The quantities consumed by males are on average higher than those consumed by females. However, similarly, males did not consume cinnamon and cocoa-flavored diets differently compared to their consumption of paste diet. These results were obtained during the choice test of 1 hr ($M_{consumption} \pm SEM$; paste diet: 0.54 ± 0.11, cinnamon diet: 0.42 ± 0.19, cocoa diet: 0.41 ± 0.16, $n = 7$)($p = 0.50$, figure 15A) but also during the choice test of 24 hr ($M_{consumption} \pm SEM$; paste diet: 3.00 ± 0.00, cinnamon diet: 2.50 ± 0.42, cocoa diet: 2.90 ± 0.10, $n = 7$)($p = 0.33$, figure 15B).

Conclusion

Our study reveals a great variability in diet consumption between individuals and the modest size of our samples does not allow us to highlight drastic differences in diet consumption, except for the protected-geraniol diet which seems less attractive than the paste diet. The protected-geraniol diet is, however, consumed at nearly 50% after 24 hr of test. In addition, if some individuals seem reluctant to consume over short periods, all diets tested at 24 hr were experienced by all individuals. These results suggest that the diets used in these experiments are generally attractive to mice, given the novelty of these foods during consumption tests and appear to be good candidates for testing STFP in this species.

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ENVIRONNEMENT SOCIO-OLFACTIF ET CHOIX ALIMENTAIRES CHEZ LA SOURIS DOMESTIQUE, *Mus musculus domesticus*

Résumé

Le succès écologique de la souris domestique, *Mus musculus domesticus*, repose en partie par sa capacité à adapter son régime alimentaire aux ressources disponibles. La transmission sociale des préférences alimentaires (TSPA) est un apprentissage observé chez les rongeurs, leur permettant d'élargir leur répertoire alimentaire à moindre risque en obtenant des informations olfactives sur de nouveaux aliments à partir des congénères. Cet apprentissage social s'observe directement, lors d'une rencontre avec un congénère ou indirectement, via des marques odorantes. Ce travail a pour but de déterminer comment les souris utilisent leur environnement socio-olfactif pour réaliser des choix alimentaires. Nos résultats ont révélé que l'absence du congénère lors de la TSPA indirecte réduit les contraintes sociales associées à une rencontre et permet l'acquisition de la TSPA entre femelles inconnues. Cependant, certaines contraintes physiques associées à la perception des informations dans les fèces peuvent réduire la disponibilité des informations alimentaires. Enfin, nous avons montré que les différentes préoccupations sexuelles des individus affectent la hiérarchisation des informations présentes dans les fèces et limitent, chez les mâles, l'acquisition de la TSPA. Nos résultats suggèrent que l'utilisation d'informations alimentaires chez les souris varie selon leur contexte social et écologique et implique différents processus tels que l'émotion et l'attention. En conditions naturelles, les voies directe et indirecte de la TSPA pourraient être complémentaires, chacune élargissant les conditions de transmission de l'information alimentaire chez les rongeurs.

Mots clés : apprentissage social, attention, perception olfactive, rongeurs

SOCIO-OLFACTORY WORLD AND FOOD SELECTION IN THE HOUSE MOUSE, *Mus musculus domesticus*

Abstract

The ecological success of the house mouse, *Mus musculus domesticus*, implies a great capacity to adapt its diet to available food resources. The social transmission of food preference (STFP) is an adaptive type of learning observed in rodents allowing them to enlarge their food repertoire at lower risk by getting olfactory information on novel food sources from conspecifics. This social learning takes place directly, during an encounter with a conspecific or indirectly, via olfactory marks. The objective of this thesis work was to determine how mice use their socio-olfactory environment to make food choices. Our results revealed that the absence of the conspecific during the indirect STFP reduces the social constraints associated with an encounter and allows the acquisition of STFP between unfamiliar conspecifics. However, some physical constraints associated with the perception of information in feces may reduce the availability of food information. We also showed that different sex concerns of individuals may affect the prioritization of information present in feces and limit, in males, the acquisition of STFP. Our results suggest that the use of food information in mice varies according to their social and ecological context and involves different processes such as emotion and attention. Under natural conditions, the direct and indirect STFP could be complementary, each of them extending the conditions for the transmission of food information in rodents.

Keywords: attention, olfactory perception, rodents, social learning

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