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Aix Marseille Université

NNT : 0000AIXM0000

THÈSE DE DOCTORAT

Soutenue à Aix-Marseille Université
le 9 décembre 2024 par

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Bases cognitives de la synchronisation comportementale chez le chien : effet des modulateurs sociaux

Discipline
Psychologie

École doctorale
ED 356 – Cognition, Langage, Education

Laboratoire/Partenaires de recherche
Centre de Recherche en Psychologie et Neurosciences (CNRS, AMU, UMR 7077)
Association Nationale de la Recherche et de la Technologie
Association Agir pour la Vie Animale

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Liste de publications et/ou brevets et participation aux conférences

1) Liste des publications et/ou brevet [a] réalisées dans le cadre du projet de thèse :

1. Lamontagne, A., & Gaunet, F. (2023). Revealing behavioural synchronization in humans and other animals: Why individuals mirror others. *Springer Nature Switzerland,* 117p. DOI: 10.1007/978-3-031-48449-0

2. Lamontagne, A., & Gaunet, F. (2024). Behavioural synchronisation between dogs and humans: Unveiling interspecific motor resonance? *Animals*, *14*(4), 548. DOI: 10.3390/ani14040548

3. Lamontagne, A., Legou, T., Bedossa, T., & Gaunet, F. (2024). Walk with me? Part 1: Dogs synchronize with an unfamiliar person who first synchronized with them. *Applied Animal Behaviour Science, 272*, 106204. DOI: 10.1016/j.applanim.2024.106204

4. Lamontagne, A., Legou, T., Bedossa, T., & Gaunet, F. (2024). Walk with me? Part 2: Dogs synchronize with an unfamiliar person who first synchronized with their owner. *Applied Animal Behaviour Science*, *275*, 106271. DOI: 10.1016/j.applanim.2024.106271

5. Lamontagne, A., Legou, T., Bedossa, T. & Gaunet. F. (accepted). Social modulation of dogs' behavioural synchronization with humans: Effect of number of people and owner's presence. *Animal Behaviour.*

6. Lamontagne, A., Legou, T., Bedossa, T. & Gaunet. F. (in preparation). Temporary title: Investigating motor interference in dogs: Incongruent human actions interfere with canine task execution.

7. Lamontagne, A., Legou, T., Bedossa, T. & Gaunet. F. (in preparation). Temporary title: Familiar congener or familiar human: Who do pet dogs best synchronize with?

[a] Cette liste comprend les articles publiés, les articles soumis à publication et les articles en préparation ainsi que les livres, chapitres de livre et/ou toutes formes de valorisation des résultats des travaux propres à la discipline du projet de thèse. La référence aux publications doit suivre les règles standards de bibliographie et doit être conforme à la charte des publications d'AMU.

2) Participation aux conférences[b] et écoles d'été au cours de la période de thèse :

1. Lamontagne, A., Legou, T., Bedossa, T. & Gaunet, F. (2024). *Exploration de la synchronisation comportementale du chien avec l'humain*. Conférence grand public organisée par l'association Brainbow, Toulouse, France. Présentation orale.

2. Lamontagne, A., Legou, T., Bedossa, T. & Gaunet, F. (2023). *Interspecific behavioural synchronization: how owner-stranger interactions affect dogs' behaviours toward the stranger.* European Veterinary Congress of Behavioural Medicine and Animal Welfare, Pisa, Italy. Présentation orale.

3. Lamontagne, A. (2023). *Effet des modulateurs sociaux sur la synchronisation comportementale de la marche du chien sur celle de l'humain*. Séminaire organisé au Laboratoire de Psychologie Cognitive, Marseille, France. Présentation orale.

4. Lamontagne, A., Legou, T., Bedossa, T. & Gaunet, F. (2023). *Effect of dogs' direct sensitivity to human social signals on dogs' behavioural synchronization.* Colloque de la Société Française pour l'Etude du Comportement Animal, Tours, France. Poster.

5. Lamontagne, A., Legou, T., Bedossa, T. & Gaunet, F. (2023). *Effect of dogs' indirect sensitivity to human social signals on dogs' behavioural synchronization.* Colloque de la Société Française pour l'Etude du Comportement Animal, Tours, France. Présentation orale.

6. Legou, T., Lamontagne, A. & Gaunet, F. (2023). *Dog monitoring system.* Colloque de la Société Française pour l'Etude du Comportement Animal, Tours, France. Poster.

7. Lamontagne, A., & Gaunet, F. (2022). *La synchronisation comportementale du chien sur le comportement de l'humain, un pilier des interactions humain-chien.* Symposium annuel de l'Association Française de Psychiatrie, Paris, France. Présentation orale.

8. Lamontagne, A., Legou, T., Rauchbauer, B., Grosbras, M.H., & Gaunet, F. (2022). *Experimental study of dogs locomotor synchronization with humans.* Ecology & Behaviour 15th meeting, Strasbourg, France. Présentation orale.

9. Lamontagne, A., Bedossa, T., & Gaunet, F. (2022). *Quels sont les modulateurs sociaux de la synchronisation comportementale ?* Agence Nationale de la Recherche et de la Technologie meeting, Paris, France. Présentation orale.

[b] Le terme « conférence » est générique. Il désigne à la fois « conférence », « congrès », « workshop », « colloques », « rencontres nationales et/ou internationales » … etc.
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Résumé

Les chiens synchronisent leurs comportements sur ceux de l'humain, cette compétence fondamentale remonte au commencement des interactions entre ces deux espèces. Chez l'humain, la synchronisation comportementale est modulée par différents facteurs sociaux. Les recherches menées dans le cadre de cette thèse révèlent que la synchronisation interspécifique (du chien sur l'humain) est également modulée par divers facteurs sociaux. En particulier, la synchronisation locomotrice de chiens sur une personne inconnue est influencée par le comportement de cette dernière : elle est temporairement améliorée si la personne a ajusté au préalable sa locomotion sur celle des chiens ou sur celle de leurs propriétaires. Le nombre d'humains affecte également l'ajustement comportemental des chiens. En effet, lorsque le propriétaire s'éloigne d'un groupe de quatre personnes, les chiens suivent le groupe plutôt que leur propriétaire, néanmoins l'effet attracteur du propriétaire finit par l'emporter sur l'effet de groupe. Enfin, le type d'agent social est aussi un modulateur de la synchronisation comportementale chez le chien, puisque les chiens se synchronisent davantage avec un congénère familier qu'avec un humain familier, bien que cet effet dépende de la présence d'autres chiens dans le foyer. Etudier la modulation sociale de la synchronisation comportementale interspécifique soulève la question des processus cognitifs sous-jacents. Une découverte remarquable résultant de ce travail de thèse est l'interférence motrice interspécifique, qui se traduit par la perturbation de l'exécution d'une action par le chien lorsqu'une action humaine incongruente est produite simultanément. Cela soutient l'hypothèse ambitieuse de la résonance motrice comme processus cognitif à l'origine de la synchronisation comportementale interspécifique. D'autres mécanismes potentiels sont également discutés. Cette thèse apporte donc des contributions théoriques significatives sur les bases cognitives de la synchronisation comportementale interspécifique, ici du chien sur l'humain. Elle ouvre également des perspectives pratiques, notamment pour la gestion des interactions chien-humain dans la vie quotidienne, dans les espaces publics, ainsi qu'en présence de personnes familières ou non.

Mots clés : Chien, Cognition, Modulation sociale, Résonance motrice, Synchronisation comportementale

Abstract

Dogs synchronize their behaviours with those of humans, a fundamental skill that dates back to the beginning of interactions between these two species. In humans, behavioural synchronization is modulated by various social factors. Research conducted during this thesis reveals that interspecific synchronization (in dogs upon humans) is also influenced by various social factors. Specifically, dogs' locomotor synchronization with an unfamiliar person is affected by that person's behaviour: it is temporarily enhanced if the person has previously adjusted their own locomotion to match that of the dogs or that of their owners. The number of humans also affects the dogs' behavioural adjustment. Indeed, when the owner moves away from a group of four people, dogs follow the group rather than their owner; however, the owner's attracting effect eventually outweighs the group effect. Finally, the type of social agent also modulates behavioural synchronization in dogs, as dogs synchronize more with a familiar conspecific than with a familiar human, although this effect depends on the presence of other dogs in the household. Studying the social modulation of interspecific behavioural synchronization raises questions about the underlying cognitive processes. A significant finding of this thesis is the evidence of interspecific motor interference, which manifests as a disruption in the dog's execution of an action when an incongruent human action is performed simultaneously. This supports the hypothesis of motor resonance as a cognitive process underlying interspecific behavioural synchronization. Other potential mechanisms are also discussed. This thesis thus provides significant theoretical contributions to understanding the cognitive foundations of interspecific behavioural synchronization, in dogs upon humans. It also opens up practical perspectives, particularly for managing dog-human interactions in everyday life, in public spaces, and in the presence of familiar or unfamiliar people.

Keywords: Behavioural synchronization, Cognition, Dog, Motor resonance, Social modulation

Remerciements

Je tiens tout d'abord à remercier les membres de mon jury, Odile Petit et Ludovic Marin, rapporteurs du manuscrit, Marine Grandgeorge, examinatrice, et Marie-Hélène Grobras, présidente du jury, pour leur disponibilité et leur engagement dans l'évaluation de ce travail de doctorat.

Je remercie mes encadrants, et tout particulièrement Florence Gaunet, ma directrice de thèse, pour ses conseils avisés et son accompagnement tout au long de ce projet. Florence, tu m'as guidée et as toujours été présente pendant la thèse, et tu m'as laissé la liberté nécessaire pour m'épanouir dans cette recherche tout en m'évitant de m'y perdre. Ta confiance a été un soutien précieux. Merci à Thierry Bedossa, qui a contribué au financement de cette thèse. Merci pour ton intérêt constant pour notre travail, enrichi par ta grande expérience de terrain. Je remercie aussi Thierry Legou pour sa bonne humeur constante et son aide technique précieuse. J'ai adoré travaillé avec toi, je garderai de très bons souvenirs de nos échanges, surtout sur la conception de la « manip tréteau ».

Un grand merci à ma famille, dont le soutien a été infaillible toutes ces années. Merci à mes parents et mes sœurs, qui m'ont encouragée à poursuivre mes rêves, depuis plus de 20 ans, où je disais déjà que « plus tard, je veux comprendre et soigner les animaux ».

Samy, je n'aurai jamais assez de mots pour te dire à quel point ton soutien indéfectible, dans les moments de joie comme dans les périodes de doute, a été important pour moi. Merci pour ta présence à mes côtés, merci pour tout.

Je remercie mes amis, pour leur présence et leur soutien quotidien. Merci aux copains de l'escalade, pour votre énergie et votre enthousiasme, impossible de ne pas être de bonne humeur en votre compagnie ! Merci aux copines vétos et du Master, pour nos moments partagés, nos goûters et nos soirées papotage. J'espère que notre amitié perdurera de nombreuses années encore.

Merci à Marine Brunel et à ses parents pour leur accueil si chaleureux et bienveillant. J'ai beaucoup appris lorsque j'étais chez vous. Marine, je suis ravie que tu reprennes le flambeau et sache que tu pourras toujours compter sur moi si besoin.

Enfin, je remercie toutes les personnes qui ont contribué, de près ou de loin, à ce projet de doctorat. Un grand merci aux propriétaires et à leurs compagnons poilus, sans qui les expériences n'auraient pas pu exister. Aux doctorants et aux autres membres du laboratoire, merci pour votre soutien. Merci à nos stagiaires, qui ont non seulement contribué aux codages comportementaux, mais qui m'ont également enrichie personnellement, en renforçant mon désir de transmettre mes connaissances et en confirmant ma vocation à devenir enseignant-chercheure.

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1. Introduction générale

Cette thèse CIFRE, co-financée par l'association Agir pour la Vie Animale (AVA) et l'Association Nationale de la Recherche et de la Technologie (ANRT), s'inscrit dans la lignée des recherches récentes ayant mis en évidence la capacité des chiens à synchroniser leurs comportements sur ceux des humains. L'objectif de ce travail de doctorat est de caractériser les propriétés de cette synchronisation comportementale interspécifique en examinant sa modulation sociale. La thèse vise ainsi à identifier les facteurs sociaux qui modulent la synchronisation comportementale chez le chien et à explorer les processus cognitifs sous-jacents. L'introduction, basée sur une monographie et une revue de questions, présente l'état des connaissances sur la synchronisation comportementale chez les espèces sociales, décrit les modulateurs sociaux étudiés au niveau intraspécifique et interspécifique, et présente le modèle de la résonance motrice interspécifique comme fondement cognitif de la synchronisation comportementale entre le chien et l'humain. Pour répondre à la problématique de la thèse, cinq études expérimentales ont été conduites. Les quatre premières portent sur l'effet de différents modulateurs sociaux, à savoir la familiarité, le nombre de personnes et le type d'agent social (intra- ou inter-spécifique), tandis que la dernière explore les mécanismes cognitifs impliqués, en évaluant l'existence de l'interférence motrice au niveau interspécifique. Les chapitres 2 à 5 s'articulent autour des articles scientifiques issus de ces expériences. La discussion générale synthétise et discute à la lueur de la bibliographie en éthologie sociale, en éthologie et cognition comparée, en psychologie cognitive et en neurosciences cognitives l'ensemble des résultats obtenus. Elle expose également les contributions théoriques, notamment au regard du modèle proposé de résonance motrice interspécifique. Elle met enfin en lumière les apports pratiques pour les propriétaires, les professionnels du monde canin et les citoyens en général.

1.1. La synchronisation comportementale chez les espèces sociales : définition, bases neurocognitives et fonctions sociales

La présente thèse porte sur la synchronisation comportementale entre le chien et l'humain. La première étape du travail de doctorat a consisté à établir une revue exhaustive des connaissances existantes sur la synchronisation comportementale chez les espèces sociales, afin de situer notre recherche dans un cadre plus large et de la contextualiser à la lumière des travaux antérieurs (Lamontagne & Gaunet, 2023). Cet état de l'art montre que la synchronisation comportementale a été largement étudiée chez de nombreuses espèces animales, pour différents comportements et dans divers contextes. Malgré la variété de définitions utilisées dans la littérature, toutes convergent sur le fait

que la synchronisation comportementale est une forme de copie de comportement dans laquelle l'aspect temporel est primordial : la synchronisation comportementale survient lorsque les individus alignent leurs comportements de façon simultanée (Lamontagne & Gaunet, 2023; Rauchbauer & Grosbras, 2020). Par exemple, les individus synchronisent spontanément leurs rythmes de marche lorsqu'ils se déplacent ensemble (Moussaïd, 2019), ou leurs balancements de jambes lorsqu'ils sont assis côté à côté sur des chaises à bascule (Richardson et al., 2012). Cette notion temporelle distingue la synchronisation comportementale des autres formes de copies de comportement, telles que l'imitation automatique. Un exemple classique d'imitation automatique est le bâillement contagieux, qui provoque le bâillement chez les observateurs avec un délai plus ou moins court (Massen et al., 2015).

La synchronisation comportementale est présente dans l'ensemble du règne animal, des insectes aux grands mammifères, en passant par les poissons et les oiseaux (Figure 1). Elle est observée à l'échelle de la dyade (deux individus), des petits groupes ou des grandes masses (Lamontagne & Gaunet, 2023). Chez les chimpanzés, par exemple, la synchronisation comportementale se produit lorsqu'ils cassent des noix : les individus alignent leur corps entre eux et exécutent simultanément l'action visant à craquer les fruits (Fuhrmann et al., 2015). Dans une expérience menée sur des macaques, japonais, il a été montré que lorsque deux singes, préalablement entrainés individuellement à appuyer sur un bouton, sont placés face à face, une synchronisation temporelle émerge. Celle-ci est caractérisée par un changement de rythme individuel jusqu'à atteindre un rythme commun de pression des boutons (Nagasaka et al., 2013).

En outre, la synchronisation comportementale se manifeste dès les premiers stades de vie et joue un rôle crucial dans le développement social des individus (Hoch et al., 2021). Chez l'humain, la synchronisation comportementale peut même survenir alors que les individus tentent de l'éviter (Issartel et al., 2007). Cette ubiquité souligne la puissance de cette forme d'alignement comportemental et l'intérêt majeur de l'étudier pour comprendre les dynamiques des interactions sociales à différentes échelles. De plus, la synchronisation comportementale est facilement observable, donc peut être aisément étudiée dans des contextes expérimentaux (Felsberg & Rhea, 2021).



Figure 1. Illustrations de la synchronisation comportementale lors d'activités de groupes au sein de diverses espèces du règne animal. Crédits : https://pixabay.com

Le support neurocognitif de la synchronisation comportementale, c'est-à-dire l'ensemble des circuits neuronaux et des processus cognitifs associés qui mènent à la production de comportements synchronisés avec ceux d'autrui, a majoritairement été étudié chez les primates. En effet, les bases neurales de la synchronisation comportementale et des autres formes de reproduction de comportements ont été mises en évidence il y a un près de 30 ans dans la zone F5 du cortex prémoteur des primates non-humains (Gallese et al., 1996). Ces neurones, qualifiés de « neurones miroirs », présentent la particularité d'être activés à la fois lorsque le sujet observe une action ou une partie de celle-ci, et lorsque le sujet exécute lui-même cette action. Quelques années plus tard, des neurones similaires ont été identifiés chez l'humain (Rizzolatti et al., 2001). Plus récemment, des neurones impliqués dans la synchronisation interindividuelle ont été mis en évidence chez des rats et des chauve-souris (Bonini et al., 2022). Néanmoins, les recherches ayant principalement porté sur les primates humains et non-humains, peu de données sont disponibles chez les autres espèces sociales. Concernant le chien, il n'y a, à ma connaissance, pas de neurones de ce type identifiés chez cette espèce à l'heure actuelle.

D'un point de vue cognitif, les recherches menées chez l'humain ont montré que la synchronisation comportementale repose sur le couplage perception-action. Plus précisément, la perception d'une action active les représentations motrices associées à cette action, entrainant l'activation des neurones miroirs (Rizzolatti et al., 2001). La perception et la production de l'action sont donc directement liées. Par ce couplage, la perception d'un comportement déclenche une première réponse automatique d'exécution du comportement perçu. Dans un second temps, c'est-à-dire après quelques centaines de millisecondes, cette première réponse est inhibée ou renforcée (Cracco et al., 2022). Si la réponse est renforcée, alors le comportement perçu est reproduit, menant à la synchronisation comportementale.

En ce qui concerne les fonctions sociales de la synchronisation comportementale, elles ont été investiguées chez diverses espèces, principalement au niveau intraspécifique. Tout d'abord, cette forme d'alignement social joue un rôle dans l'apprentissage social (Fuhrmann et al., 2015). En effet, en observant un individu réaliser un comportement nouveau, l'observateur peut tenter de le copier. Se synchroniser avec cet individu favorise ainsi la transmission de comportements. Également, la synchronisation comportementale contribue à l'identification des actions, comme cela a été démontré, par exemple, chez les chiens (Marshall-Pescini et al., 2014 ; Piotti & Kaminski, 2016) et les pigeons (Asen & Cook, 2012). Identifier les actions de l'autre permet aux individus d'adapter leur propre comportement pour maintenir la synchronisation, ce qui confère donc à la synchronisation comportementale une forte valeur adaptative (Duranton & Gaunet, 2016). Par ailleurs, chez l'humain, la synchronisation comportementale a une fonction sociale de plus haut niveau : elle contribue à la reconnaissance du but d'une action, voire des intentions de la personne qui l'exécute (Iacoboni et al., 2005). Chez les espèces sociales non-humaines, l'attribution d'intentions reste controversée, car elle est difficilement objectivable. Par conséquent, les fonctions sociales de haut niveau de la synchronisation comportementale ne sont à l'heure actuelle pas reconnues chez les animaux non humains (Birch et al., 2020).

Des informations plus détaillées sur les bases neurales et cognitives de la synchronisation comportementale et sur ses fonctions sociales sont fournies dans les chapitres 1 à 5 de la monographie :

Lamontagne, A., & Gaunet, F. (2023). Revealing behavioural synchronization in humans and other animals: Why individuals mirror others. *Springer Nature Switzerland*, 117p. https://link.springer.com/book/10.1007/978-3-031-48449-0

1.2. La modulation sociale de la synchronisation comportementale interspécifique

1.2.1. Etat de l'art sur les modulateurs sociaux de la synchronisation comportementale

La synchronisation comportementale ne survient pas constamment ni dans tous les contextes. D'ailleurs, une copie excessive et inappropriée des comportements d'autrui constitue chez l'humain un trouble neurologique, connu sous le nom d'échopraxie, et serait lié à un défaut d'inhibition des neurones miroirs dans le cortex préfrontal (Rizzolatti et al., 2009). Examiner les conditions dans lesquelles la synchronisation comportementale est modulée est donc crucial pour comprendre les processus cognitifs qui permettent sa mise en place.

Pour étudier la modulation sociale de la synchronisation des comportements moteurs du chien par rapport à l'humain, il est d'abord essentiel d'identifier les modulateurs sociaux potentiels. A cette fin, une revue exhaustive de la littérature a été menée pour recenser les modulateurs sociaux observés chez différentes espèces. Nous avons ainsi listé les facteurs, résumés ci-après, qui influencent la synchronisation comportementale, en fonction des caractéristiques des individus en interaction. Nous avons notamment relevé le rôle de l'état attentionnel : plus les individus sont attentifs à l'autre, plus la synchronisation est facilitée (Bente & Novotny, 2020). La distance interindividuelle est également déterminante, il s'agit de l'une des composantes de la synchronisation comportementale et elle est liée aux deux autres : plus les individus sont proches, plus ils ont tendance à synchroniser leur activité (McDougall & Ruckstuhl, 2018). Le niveau de familiarité entre les individus est un autre modulateur social, en effet les individus familiers se synchronisent davantage entre eux que des individus non familiers (Shamay-Tsoory et al., 2019). De même, l'appartenance à un groupe a un effet sur la synchronisation comportementale, puisque les membres d'un même groupe se synchronisent davantage entre eux qu'avec des individus extérieurs au groupe (Shamay-Tsoory et al., 2019). Le leadership joue également un rôle, chez les espèces vivant en groupe, pour lesquelles les individus se synchronisent plus souvent sur les leaders que sur les autres individus (Rinott & Tractinsky, 2021). D'autres modulateurs de la synchronisation comportementale ont été étudiés spécifiquement chez l'humain, comme l'influence sociale : nous nous synchronisons plus facilement sur des personnes qui exercent une influence sur nous que sur celles qui n'en n'exercent pas. Les enfants par exemple se synchronisent davantage sur les enseignants que sur d'autres adultes familiers (McGuigan, 2013). L'effet du profil visuomoteur a également été étudié chez l'humain, les recherches ayant notamment démontré que les individus présentant des caractéristiques motrices similaires atteignent plus rapidement la synchronisation que des individus ayant des caractéristiques motrices différentes (Nessler & Gilliland, 2009). Enfin, la synchronisation comportementale est également modulée par le nombre

d'individus et la conformation du groupe ; elle est par exemple de plus haut degré à mesure que la taille du groupe augmente (Moussaid et al., 2009).

Des informations plus détaillées sur les modulateurs sociaux de la synchronisation comportementale sont fournies dans le chapitre 6 de la monographie : Lamontagne, A., & Gaunet, F. (2023). Revealing behavioural synchronization in humans and other animals: Why individuals mirror others. *Springer Nature Switzerland*, 117p. https://link.springer.com/book/10.1007/978-3-031-48449-0

La revue de la littérature présentée précédemment constitue une base solide pour évaluer les modulateurs sociaux déjà étudiés au niveau interspécifique, identifier les lacunes existantes et déterminer les modulateurs à investiguer. Elle permet également de nous appuyer sur les méthodologies employées dans la littérature pour élaborer nos protocoles expérimentaux. A partir de cette revue, nous avons identifié plusieurs modulateurs sociaux potentiellement pertinents : l'effet de la familiarité, l'effet du niveau d'activité, l'effet du nombre d'agents, l'effet du profil locomoteur et l'effet du type d'agent social. Compte tenu de la durée limitée d'une thèse, il était impossible de tester tous ces modulateurs. Il était donc impératif de réaliser une sélection judicieuse des modulateurs d'intérêt, en utilisant des critères de pertinence théorique, d'apport pratique, de faisabilité et de quantifiabilité dans un cadre expérimental. L'effet de la familiarité avait déjà été étudié, les recherches antérieures ayant révélé que le degré de synchronisation dépendait du niveau de familiarité entre le chien et l'humain (Duranton et al., 2016, 2019a, 2019b). Puisque les chiens sont fréquemment en contact avec des personnes non familières, nous avons décidé d'explorer l'effet du comportement d'une personne non familière, en particulier sa synchronisation sur le chien ou sur son propriétaire. Nous avons également testé l'effet du nombre de personnes entourant le propriétaire du chien, car les résultats des études existantes sont divergents (Lamontagne et al., 2023; Nagasawa et al., 2020). De plus, ce modulateur présente un intérêt théorique pour comprendre les mécanismes sous-jacents à la synchronisation comportementale (Cracco & Brass, 2018). Enfin, nous avons examiné l'effet du type d'agent social, en comparant la synchronisation comportementale entre chiens et entre le chien et l'humain, car cela offre des perspectives pour comprendre la phylogénie de la synchronisation comportementale. En revanche, nous n'avons pas testé l'effet du niveau d'activité, en raison des difficultés de mise en œuvre pour garantir un niveau d'activité uniforme au sein des groupes expérimentaux. Nous n'avons pas non plus testé l'effet du profil locomoteur par crainte que le recrutement de personnes présentant un profil locomoteur spécifique (tel que celui d'une personne ayant un déficit locomoteur par exemple) ne conduise à des échantillons trop réduits.

1.2.2. Investiguer les processus cognitifs en jeu : l'hypothèse de la résonance motrice interspécifique, cas de *Canis Familiaris*

L'espèce canine est divisée en quatre catégories en fonction de l'environnement de vie. Les chiens de compagnie vivent dans les foyers humains dès leurs premiers stades de vie et partagent quotidiennement des activités avec l'humain (Poresky & Daniels, 1998). Les chiens de travail sont également en contact étroit avec l'humain mais recoivent un haut niveau d'entraînement pour accomplir des tâches spécialisées, comme l'assistance aux personnes en situation de handicap (Bray et al., 2021). Les chiens de refuge ont connu la présence humaine mais vivent dans des conditions qui limitent les interactions avec l'humain (Protopopova, 2016). Enfin, les chiens féraux n'ont pas de contacts rapprochés avec l'humain, ils ne sont en conséquence pas exposés aux activités humaines (Contreras-Abarca et al., 2022). Dans cette thèse, nous nous sommes focalisés sur les chiens de compagnie car ils constituent un modèle prometteur pour étudier les propriétés de la synchronisation comportementale entre espèces. En effet, les chiens de compagnie sont issus d'une espèce sociale qui partage l'environnement de l'humain depuis des millénaires. De plus, de par leur environnement de vie, les chiens de compagnie dépendent des humains et interagissent quotidiennement avec eux, souvent davantage qu'avec leurs congénères (Gaunet et al., 2014). La recherche en cognition sociale canine, qui connait un intérêt scientifique croissant, a révélé que les chiens de compagnie possèdent des capacités cognitives comparables à celles de l'humain, comme la communication référentielle, ou la surimitation (Duranton & Gaunet, 2018). Considérant cela, il est possible que la synchronisation comportementale entre le chien et l'humain repose sur des bases cognitives similaires à celles présentes chez l'humain. Nous avons ainsi formulé l'hypothèse que la résonance motrice interspécifique soit le fondement neurocognitif de la synchronisation comportementale entre le chien et l'humain. L'article ci-après a pour but de présenter les arguments qui ont conduit à cette hypothèse, tout en offrant des perspectives de recherche pour en évaluer la validité.

Article 1 : Lamontagne, A., & Gaunet, F. (2024). Behavioural synchronisation between dogs and humans: Unveiling interspecific motor resonance? *Animals, 14*(4), 548.

https://doi.org/10.3390/ani14040548

animals

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Review

Behavioural Synchronisation between Dogs and Humans: Unveiling Interspecific Motor Resonance?

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Simple Summary: It is widely acknowledged that dogs synchronise their behaviours with those of humans. In this article, we delve into the neural and cognitive bases of this form of behavioural adjustment. Using knowledge of cerebral processes underlying behavioural synchronisation in humans, namely motor resonance and the activation of mirror neurons, we investigated whether dogs' behavioural synchronisation with humans could be based on similar mechanisms. In humans, both perceiving and executing an action activate the motor representations of that action. Motor resonance occurs when motor representations of an action are simultaneously activated in both the observer and the individual being observed. Mirror neurons are the neural substrate for motor resonance as these motor neurons activate both when an individual performs or perceives an action. Our review of existing literature shows that motor resonance could occur in dogs, suggesting that dogs' behavioural synchronisation with humans relies on the activation of both human and canine mirror neurons. Behavioural studies suggest but do not prove the existence of motor resonance between the two species, and thus further research is needed to confirm this hypothesis. Revealing the mechanisms underlying dogs' behavioural synchronisation with humans would contribute to a better understanding of how dogs and humans have evolved together since the beginning of their cohabitation.

Abstract: Dogs' behavioural synchronisation with humans is of growing scientific interest. However, studies lack a comprehensive exploration of the neurocognitive foundations of this social cognitive ability. Drawing parallels from the mechanisms underlying behavioural synchronisation in humans, specifically motor resonance and the recruitment of mirror neurons, we hypothesise that dogs' behavioural synchronisation with humans is underpinned by a similar mechanism, namely interspecific motor resonance. Based on a literature review, we argue that dogs possess the prerequisites for motor resonance, and we suggest that interspecific behavioural synchronisation relies on the activation of both human and canine mirror neurons. Furthermore, interspecific behavioural studies highlight certain characteristics of motor resonance, including motor contagion and its social modulators. While these findings strongly suggest the potential existence of interspecific motor resonance, direct proof remains to be established. Our analysis thus paves the way for future research to confirm the existence of interspecific motor resonance as the neurocognitive foundation for interspecific behavioural synchronisation. Unravelling the neurocognitive mechanisms underlying this behavioural adjustment holds profound implications for understanding the evolutionary dynamics of dogs alongside humans and improving the day-to-day management of dog–human interactions.

Keywords: dog; human–animal interaction; behaviour; synchronisation; motor resonance; mirror neurons; motor contagion; interspecific cognition

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Citation: Lamontagne, A.; Gaunet, F. Behavioural Synchronisation between Dogs and Humans: Unveiling Interspecific Motor Resonance? *Animals* **2024**, *14*, 548. https://doi.org/10.3390/ani14040548

Academic Editor: Mandy Paterson

Received: 1 December 2023
Revised: 5 February 2024
Accepted: 6 February 2024
Published: 7 February 2024

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1. Introduction

Behavioural synchronisation occurs when individuals exhibit the same behaviour in the same location and at the same time. This form of behavioural alignment is widely documented and ubiquitous in social species (see [1,2] for comprehensive reviews). Dogs, like many social species, exhibit behavioural synchronisation at the intraspecific level. During group activities, such as play sessions or when moving in a pack, dogs copy the behaviour of their peers and behave synchronously by staying close to each other, ex- changing glances and vocalising [3–5]. These behaviours are the cornerstone of dogs' social interactions. Dogs, however, hold a unique and significant role in human history, marking the earliest instance of domestication, over 20,000 years ago [6–10]. The process of domestication involved the close coexistence of wolves, the ancestors of dogs, and humans, sharing territory and living closer and closer together over time [11]. These wolves were predators and ate the same prey as humans. Selected wolves were fed and raised by humans and became increasingly dependent on humans [12]. They then assisted humans in tasks such as hunting livestock protection. Archaeological evidence indeed reveals that through domestication, dogs maintained close contact with humans, living near them, initially scavenging human food remains and later participating in hunting expeditions [13,14]. Genomic analyses provide compelling evidence of the enduring and close relationship between dogs and humans [6,7,10,15–17]. These analyses reveal that dogs often accompanied groups of humans on their journeys, although instances exist where humans ventured without their canine companions. Dogs traversed between hu- man communities, or their presence was a result of cultural and economic exchanges [6]. This shared history has entrenched dogs as ubiquitous members of human communities worldwide, serving as companions, working partners, or cohabitants within villages [16]. Today, dogs have indeed become ubiquitous in human environments; they are able to adapt socially and spatially to urban living [18,19]. In many societies, dogs are no longer considered solely as working animals but also as members of households, sharing many daily activities alongside humans [14,19]. The millennia that dogs and humans have spent in cohabitation have led dogs to develop specific cognitive capabilities [20,21]. Notably, dogs are sensitive to human behavioural cues, following the direction of humans' gazes or pointing gestures. They are also capable of referential communication with humans [22–26]. More recently, studies have revealed that dogs synchronise their behaviour with that of humans, using the example of locomotor synchronisation, i.e., the synchronisation of loco- motor behaviours. A key part of human–dog interactions involves dogs walking alongside humans: humans and dogs walk together in many everyday situations [19,27,28]. In urban settings, dog owners take their dogs on two to four daily walks around their neighbour- hood and walk or run with their canine companions; during their walks, dogs and owners mutually adjust their walking pace to each other. Experimental studies have demonstrated that dogs spontaneously synchronise their locomotor behaviour with their owners during off-leash walks without explicit reinforcement, whether indoors or outdoors, in known or unknown environments [20,29–32]. Interspecific behavioural synchronisation between dogs and humans is thus well documented. However, the existing body of research has focused on demonstrating this form of behavioural alignment but has not delved into its underlying neurocognitive mechanisms. Given the distinctive cognitive abilities observed in dogs, we can reasonably assume that behavioural synchronisation between dogs and humans shares similar neurocognitive underpinnings with that observed in human–human interactions. In humans, behavioural synchronisation hinges on motor resonance, i.e., the simultaneous activation of motor representations in interacting individuals (see [33] for a recent and emblematic review). Motor resonance is linked to action perception coupling and is associated with the activation of mirror neurons. The current review aims to offer a comprehensive examination of the existing literature on the underlying mechanisms of behavioural synchronisation, in an effort to determine whether action perception coupling and mirror neurons might serve as the neurocognitive underpinnings for dog–human be- havioural synchronisation. Furthermore, we will explore the properties of motor resonance,

including motor contagion and its modulation, to ascertain the consistency of findings in interspecific studies with these fundamental properties. This review represents the first exploration of the mechanisms underlying interspecific behavioural synchronisation, ultimately contributing to our understanding of the intricate co-evolutionary relationship between dogs and humans.

2. Sensorimotor Prerequisites of Motor Resonance

2.1. The Case of Humans

Humans, like other social species, tend to align their behaviours with one another (see [34] for a review on behavioural alignment in humans). Behavioural synchronisation is a form of behavioural alignment, like mimicry and automatic imitation. Neurological studies conducted in humans found that behavioural alignments rely on motor reso- nance [35–39]. The concept of motor resonance originates from the field of physics and is used to describe the phenomenon in which one system oscillates at the same frequency and in phase with another system [40]. When applied to social interactions, motor reso- nance occurs when the motor systems of interacting individuals are in phase. Specifically, when individuals mutually align their behaviours, the sensorimotor representations associ- ated with these behaviours are activated simultaneously in the brain of each interacting individual [40].

As far as we know, motor resonance and its prerequisites have only been studied in humans. To achieve motor resonance, people must be capable of perceiving the behaviour of others. In other words, perceiving others' behaviours is necessary for motor resonance to occur. The perception of another person's action activates sensory representations associated with that action in the observer. These sensory representations then activate motor representations related to the observed action [41]. In other words, sensory perception is translated into an internal representation in the observer's brain, first sensory, and then motor [42]. This activation is triggered through the Action Observation Network (AON), which encodes observed actions into the motor program (see Figure 1) [43]. This network automatically activates when perceiving an action. With this network, motor representa- tions are activated following action perception, and thus, motor resonance occurs, making observers more inclined to perform the action themselves [35,44,45]. The perception of an action thus directly influences the motor response. Furthermore, the perception of action and the production of action share a common representational format. The cor- respondence between perceived and executed actions corresponds to action perception coupling [42]. Perception and action are thus not distinct and independent processes but are interconnected and interdependent (see Figure 1) [45].

Hence, when individuals interact, a system is in place to detect social alignment or misalignment, and this process relies on the perception of the other's behaviour [46]. A two-stage process then comes into play (see Figure 1) [47,48]. The first stage is a bottom-up process: the perception of the behaviour induces a corresponding state in the observer, leading to motor resonance as described above. This first stage prompts a rapid response characterised by a tendency to reproduce the perceived behaviour [47]. This early response was demonstrated in a transcranial magnetic stimulation study, revealing a stimulus-driven mirror response in the subjects' motor cortex within 150 ms of the onset of the observed behaviour [49]. Following this first stage, top-down processes reinforce or inhibit the initial response. These processes are contingent upon various factors related to the observer and the people initially producing the behaviour (see [2] for an exhaustive review of these social factors). This leads to another, later motor cortex response, around 300 ms after the behaviour is perceived [45]. If this second stage reinforces the initial response, then motor resonance is not inhibited, resulting in the observer performing the perceived behaviour [41]. This behavioural response triggers brain reward circuits, strengthening the mutual adjustment between individuals and enhancing their social relationship [46]. Being able to perceive and decode the behaviours of others is thus a prerequisite of motor resonance and allows one to adapt one's own behavioural response [50]. Note that this ability

can be impaired, as in the case of ideomotor apraxia, for example. This neuropsychological disorder is caused by a cortical lesion, characterised by a loss of the ability to perform a gesture on demand or to imitate a perceived action [51].

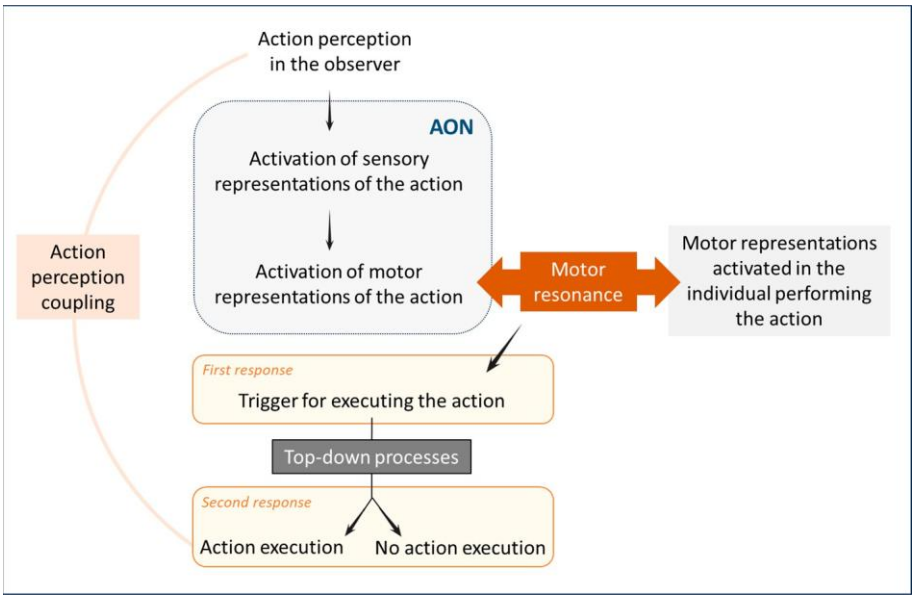


Figure 1. Sensorimotor processes associated with motor resonance in humans. The perception of an action activates the observer's sensory and motor representations associated with that action. Motor resonance induces a first response, which is a trigger for executing the action. This initial response is modulated through top-down processes, either reinforcing or inhibiting it. When this initial response is uninhibited, it leads to the observer executing the perceived action.

The importance of perception in achieving motor resonance is emphasised by the fact that motor resonance depends on individuals' level of attention. When people are fully attentive to each other, motor resonance occurs; if they are not entirely attentive to each other, motor resonance is reduced [43]. In a neurophysiological study, the amplitude of subjects' motor responses was lower when they were instructed to simultaneously monitor the activity of an LED light while observing rhythmic hand movements, compared to a condition in which subjects solely observed the hand movements [43]. Behavioural studies also demonstrate that a certain level of attention between the interacting partners is necessary to achieve behavioural synchronisation [52–54]. For example, individuals seated in rocking chairs exhibited less synchronisation in their rocking movements when positioned side by side, when they were unable to see each other, in contrast to when they were face to face and could be visually attentive to each other [55]. Attention toward a social agent is thus a prerequisite for motor resonance to occur.

2.2. Are Prerequisites of Motor Resonance Present in Dogs?

Individuals need to be able to perceive and decipher the actions of others to experience motor resonance. In social species, individuals are able to discriminate the behaviours of their congeners; this capacity is necessary for communication. Like all social species, dogs have the ability to discriminate the behaviours of their conspecifics and take this information into account to adjust their own behaviours [56–58]. During pack conflicts, for instance, dogs observe their packmates, which is interpreted as a means to recruit them for combat or to coordinate their movements for synchronised collective action [56]. This ability is also observed when dogs hunt. Hunting in canids is based on the transfer of information between individuals during group movements [59,60] and as observed in African Wild Dogs, it implies that individuals focus their attention on a single prey and relate to one another in space and time [61,62]. Dogs, like other canids, are able to identify

the position and activity of their partners in order to hunt cooperatively. When pursuing prey, a few individuals hide in ambush, waiting for other pack members to bring the prey toward them. A relay run can also occur during pursuit; this is a type of cooperative running in which canids alternately play different roles in the hunting activity [63]. The motor sequence of canids hunting is triggered by the movement of the prey, after which canids display specific behaviours: they move toward the prey, then pursue it by fanning out, approaching it, and circling it until it becomes motionless (see Figure 2) [63].

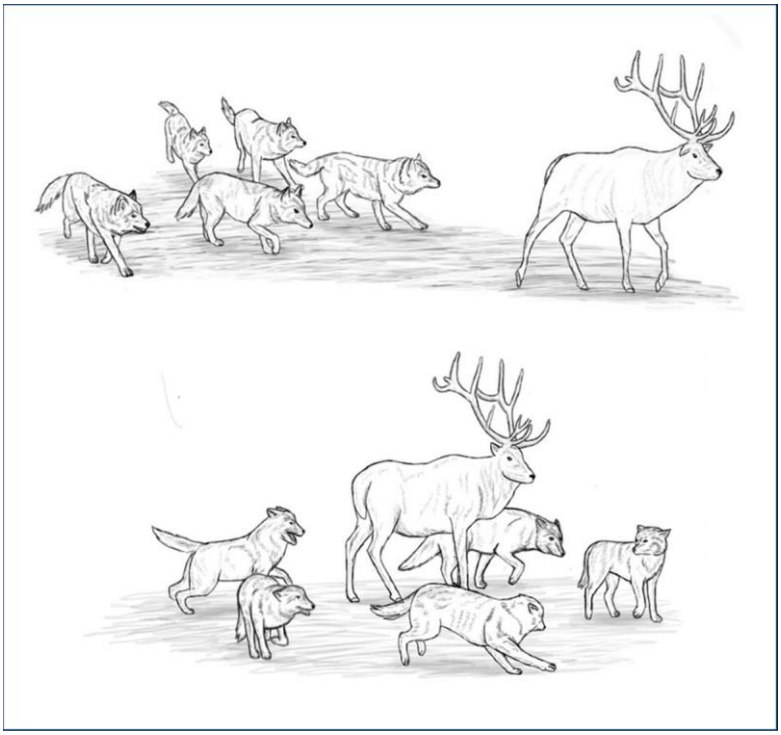


Figure 2. Canine behaviours while hunting.

Dogs distinguish not only the behaviours exhibited by other dogs but also those performed by humans. The process of domestication led to the selection of specific canine cognitive abilities toward humans, a process which has been the subject of numerous studies in recent decades. It is widely accepted that dogs perceive and copy some human behaviours. For instance, studies using the "Do as I do" procedure showed that dogs learned to copy actions demonstrated by humans such as turning around or jumping over an obstacle and then could generalise it to other human behaviours they had not specifically been taught, like opening a door or moving an object [64,65]. Dogs were also found to copy human actions even when they were not causally relevant: dogs copied their owner pushing a door leading to a food reward, but they also copied their owner touching coloured dots next to the door, even though it did not give them access to the food [20]. Lastly, another study showed that when faced with a stranger, dogs copied their owner's behaviour, by approaching the person or staying back based on their owner's behaviour [66]. Dogs are sensitive to human behavioural cues: they follow gaze direction, pointing gestures, and head orientations [21,67,68] and discriminate facial expressions [69] and body postures [50,70]. Dogs adjust their behavioural responses based on perceived human cues [20,26,71,72]. For example, they perform better at reaching a reward hidden behind a fence when the action is first demonstrated by a human than when there is no human demonstration [73]. Similarly, when a person hides food under one of several containers out of sight of the dogs and then points to indicate the location of the hidden treat, dogs follow the indicated direction to find the food [74]. Dogs are also capable of adapting their behavioural responses according to the human's attentional state. In

an experiment, dogs were presented with a visible and accessible food reward, but an experimenter prohibited them from touching the food [75]. The experimenter then either continued to look at the dog, left the room, turned their back, engaged in a distracting activity, or closed their eyes. Dogs' behaviours varied depending on the person's attentional state. Notably, the dogs approached the food less, disobeyed less frequently, and sat more often when the experimenter was looking at them compared to the other conditions. In another experiment, dogs were placed in a room and could see an inaccessible reward. They then positioned themselves optimally in relation to the height of the reward and the owner's line of sight [23].

When dogs are presented with new situations, they seek information from their owners and adjust their behavioural responses based on perceived behaviours; this is known as social referencing [76,77]. These studies show that when faced with an unfamiliar object, dogs looked at their owner in a referential manner and adjusted their behaviour based on their owner's reaction toward the object. Dogs approached the object more quickly when their owner had a positive facial expression compared to when the owner displayed a negative facial expression toward the object. Social referencing, initially studied in human dyads of young children and their mothers, thus also occurs in dog–owner dyads. Another capacity that was previously believed to be uniquely human and that has been observed during dog–human interactions is overimitation [78–80]. This behaviour occurs when an individual copies another individual's action, even when the action is causally irrelevant. Overimitation has not been observed in other primate species and until it was observed in dogs during dog–human interactions, only humans were thought to be capable of copying irrelevant or functionally unnecessary actions demonstrated by a conspecific. Because dogs possess all these cognitive processes, they thus also possess the prerequisites for motor resonance in their interactions with humans. Dogs discriminate human behaviours, are sensitive to their attentional state, and adapt their motor responses based on perceived human social cues. They adjust their behaviours to those of humans, both in familiar contexts and in novel situations. It therefore seems reasonable to assume that behavioural synchronisation between dogs and humans is based on a mechanism akin to that occurring during human interactions, namely interspecific motor resonance.

3. Mirror Neurons, the Neuronal Substrate of Motor Resonance

3.1. Mirror Neurons and Interbrain Synchronisation in Primates

Mirror neurons were discovered three decades ago in the F5 area of the premotor cortex in monkeys [81–84]. Neurons homologous to those identified in the F5 region of primates were subsequently found in humans, notably in Brodman's area, the superior parietal lobe, the inferior parietal lobe, the dorsolateral prefrontal cortex, the parietal cortex, and the premotor cortex [35,85–87]. The distinctive feature of mirror neurons is their activation both when a subject performs an action and when the subject observes another individual performing the same action [88]. Initially, mirror neurons were thought to respond exclusively to goal-directed actions [35,84]. Subsequent studies have identified additional properties of mirror neurons (see [89] for a review). Mirror neurons can respond to both observed actions and visually presented objects, to actions performed with a tool, and to nonbiological objects in motion. In monkeys, for example, cells in the lateral intraparietal area are activated both when the monkey looks in the preferred direction of the neuron and when another monkey looks in the same direction [90]. There are also canonical neurons in the ventral premotor cortex of monkeys that activate when the individual performs an action directed at an object and when the individual perceives the object as the target of the action [91]. Mirror neurons are therefore sensorimotor neurons with both motor and perceptual properties [91]. These neurons provide neurophysiological support to action perception coupling, as they fire during both the perception and execution of actions, proving the interconnection between motor and sensory areas [35,82,84,92]. When an individual observes a conspecific performing an action, the observer's mirror neuron activity reflects the mirror neuron activity of the individual executing the action [91]. Mirror neurons are

thus the neural underpinning for motor resonance. Neurophysiological studies support the correspondence of brain activity between interacting individuals. In early neurophysiological studies, the measurement techniques did not allow researchers to simultaneously record brain activity in multiple subjects during social interactions [86,93,94]. These studies were limited to single-brain recordings and did not focus on interbrain dynamics during social interactions. More recent studies have adopted innovative methodologies such as hyperscanning, portable electroencephalography (EEG), or wireless functional near-infrared spectroscopy (fNIRS), which can simultaneously record brain activity in all interacting individuals [95–99], making it possible to understand when and how neural processes become synchronised between two or more people [99,100]. These advanced approaches have revealed that brain activity in interacting individuals is synchronised during social engagement [96,101]. For example, an EEG study assessing neural coherence in a classroom of teenagers demonstrated that the degree of synchronisation of brain activity between students predicted both student engagement and social dynamics in the classroom [95]. An fNIRS study showed increased intercerebral activity synchronisation in the premotor cortex when two subjects engaged in a finger-tapping synchronisation task compared to a control task without interaction [97]. Another fNIRS study showed greater synchronisation of intercerebral activity in the right superior frontal cortices in participants during a cooperative computer game compared to a competitive game [102]. This improved synchronisation was associated with better player performance. Other studies have shown intercerebral synchronisation in the frontotemporal region and temporoparietal junction when individuals are engaged in social interactions [95,103–106]. Finally, neurophysiological studies show that interbrain synchronisation involves motor regions and areas associated with attention, suggesting that this synchronisation depends in part on the mutual recognition of a partner's role and actions and is associated with shared attention [42,91,103,107,108].

In sum, the discovery of mirror neurons has provided neural evidence for motor resonance in human and non-human primates. Although mirror neurons have been the subject of numerous studies and debates regarding their social function (see [89,109] for reviews), it is widely acknowledged that mirror neurons have a role in imitative processes, including behavioural synchronisation. Mirror neuron activation promotes motor resonance and intercerebral synchronisation, leading to interindividual behavioural synchronisation if the context of social interaction is appropriate: when individuals are affiliated, mutually attentive or share a common goal, for instance.

3.2. Do Dogs Possess Mirror Neurons? Drawing Insight from Mirror Neurons in Other Social Species

Thus far, mirror neurons have not been explicitly identified in dogs, but the evolutionary continuity of mammalian brains implies that mirror neurons may be present in all mammalian brains [110]. Indeed, brain areas involved in imitation and prosocial systems have been conserved over evolutionary time for many mammalian species [111]. This neurological conservation suggests that this behavioural mechanism is built upon an evolutionary ancient mechanism of motor resonance. Motor resonance would therefore be based on automatic action perception coupling in sensorimotor brain areas [112]. To date, in primate species and rodents, neurons encoding observed actions [113], emotions [114], and direction of attention [90] have been found in brain areas dedicated to the processing of self-related information [89]. For example, a recent study demonstrated that distinct neural populations in the prefrontal cortex in mice drive interbrain neural synchronisation during dyadic social interactions [115]. This interbrain neural synchronisation plays a role in behavioural synchronisation and maintaining social interaction. Another study showed that mirror neurons can be activated at the interspecific level in primates, as macaques recognise when their goal-directed actions are imitated by a human experimenter [116].

Moreover, additional experimental evidence demonstrates that mirror neurons are not only present in mammalian species, as they have been found in songbirds as well [117,118]. Researchers have found audiovocal neurons in birds with properties similar to those of mir-

ror neurons in the premotor cortex in primates. These neurons exhibit audiovocal mirroring properties during the perception of auditory information. This homology suggests a phylogenetic origin of neurons related to the self and the actions of others, a solution conserved over evolution for imitation and social learning in social species (see Figure 3) [89].

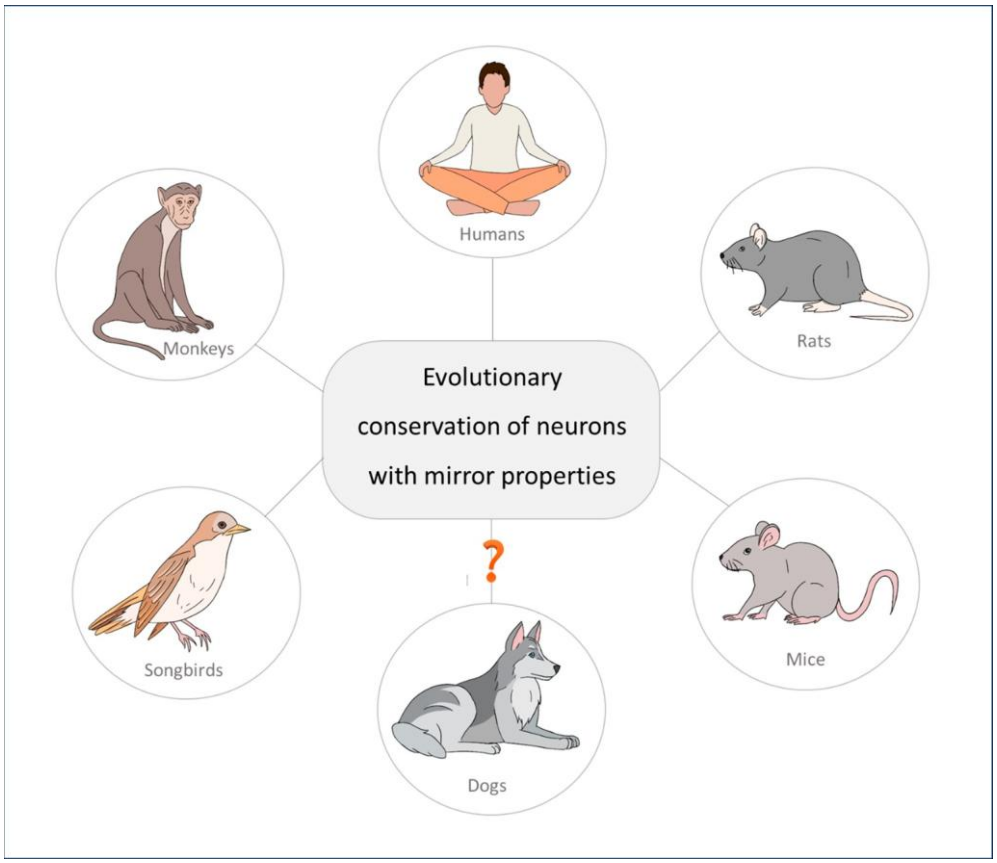


Figure 3. Mirror neurons, a neurological solution conserved over evolution for behavioural alignment in social species.

This set of evidence strongly suggests that dogs also possess mirror neurons. Given the neurological conservation of the mirror system and the cognitive abilities of dogs toward social cues and human actions, it is conceivable that due to their extensive history of living alongside humans, dogs have developed cerebral representations of actions akin to those of humans, resulting in a set of representations of actions common to both dogs and humans [119]. Consequently, it becomes entirely plausible that human mirror neurons, on the one hand, and canine mirror neurons, on the other, could be activated during dog–human interactions involving behavioural alignment. Interspecific behavioural synchronisation would then be based on interspecific motor resonance. Neurophysiological and behavioural studies are needed, however, to substantiate this hypothesis.

4. Evidence for Motor Resonance from Behavioural Studies

4.1. Motor Resonance and Motor Contagion

In humans, when the automatic response triggered by motor resonance is not inhibited, it results in the execution of the corresponding action by the observer (see Figure 1). There is thus a spread of behaviours from the observed person to the observer [120]. This is known as motor contagion: a behaviour is propagated from one individual to another through sensorimotor entrainment [121]. Motor contagion leads to behavioural synchronisation if the observed individuals continue to exhibit their behaviour, resulting in interacting individuals performing the same behaviour simultaneously. Alternatively, it leads to rapid

mimicry if the observed individuals cease their behaviour and are quickly mimicked by the observers [109]. Motor contagion is therefore the behavioural result of motor resonance in species possessing a mirror neuron system [122]. Demonstrating motor contagion within the context of dog–human interactions would provide supporting evidence for the existence of interspecific motor resonance. In dogs, the spread of behaviours can be observed at the intraspecific level during play interactions, when dogs produce play solicitation behaviours, lowering the front of their body toward the ground and opening and relaxing their mouth; these behaviours are then quickly copied by their conspecifics [3]. At the interspecific level, numerous studies have examined the spread of behaviours in dogs during their interactions with humans. We will present two examples: contagious yawning, a case of motor contagion leading to rapid mimicry, and contagious locomotor behaviours, a case of motor contagion leading to behavioural synchronisation.

The contagion of yawning has been the subject of many studies (see [123] for a review) as it is a classic example of motor contagion. In human and non-human primates, the perception of yawning via visual and/or auditory cues triggers yawning in the observer [5,124–127] through the activation of the mirror neuron system [128]. Contagious yawning has also been studied at the interspecific level between chimpanzees and humans and between dogs and humans. The perception of human yawning has been shown to induce yawning in young chimpanzees but not in infant chimpanzees [129,130]. Similarly, contagious yawning has not been found in puppies when they perceive human yawn- ing [131]. Some studies on adult dogs have reported that yawning is contagious when dogs visually and/or auditorily perceive familiar or unfamiliar human yawning [5,132–134]. However, other studies have found different results indicating the absence of contagious yawning when dogs perceive human yawning [135,136]. These discrepancies may stem from the fact that the function of yawning is not clearly established [137,138]. Yawning may have a different social function in humans and dogs, which could explain the variability in study results.

Other studies have highlighted locomotor contagion during dog–human walks. Dogs and humans have been walking together for millennia, and there is no ambiguity about the function of walking behaviour: to move from one location to another. Studies on dog locomotor synchronisation with humans have shown that locomotor entrainment occurs when dogs perceive humans walking [29–32]. The results of these studies indicate that when a dog's owner starts moving, this induces the dog to move within a few seconds (see Figure 4). This locomotor contagion occurs whether the dog is in an indoor or outdoor space, known or unknown to the dog, and whether the owner is alone or in a group of people (see Figure 4). This locomotor contagion then enables dogs to synchronise their locomotion with their owners: when owners change their walking pace, dogs adapt their own pace within about 2 s. In humans, locomotor contagion relies on motor resonance and the activation of mirror neurons [46,139–141]. Individuals then synchronise their locomotion to reduce discrepancies between representations of the observed motor behaviour and their own behaviour [142]. Locomotor contagion in dog–human interactions could conceivably rely on a similar mechanism, namely interspecific motor resonance.

Our hypothesis proposes that the locomotor contagion from humans to dogs arises from an interspecific motor resonance mechanism. However, it is crucial to acknowledge the possibility that this phenomenon might also result from a process that does not necessarily involve the activation of canine mirror neurons during the perception of human actions. While it is highly likely that dogs possess mirror neurons, it remains possible that these neurons do not activate in interspecific interactions. The dogs' perception of human action would then not trigger the canine motor areas associated with that action but rather other cerebral areas, such as cerebral reward circuits, prompting dogs to mimic humans without relying on sensorimotor entrainment. The contagion of locomotor behaviours would then stem from an associative learning process [143]. Indeed, dogs quickly form stimulus–reward associations [144], and human cues can be reinforcers for dogs [145], so dogs may walk with their owner only because it is rewarding for them. Neurophysiological studies

are thus essential to validate or refute our hypothesis of interspecific motor resonance. Investigating the areas activated in dogs' brains when perceiving human behaviours, such as walking, and comparing them to those activated during the dogs' own walking could unveil whether the locomotor synchronisation between dogs and humans is indeed a result of interspecific motor resonance or if alternative mechanisms are at play.

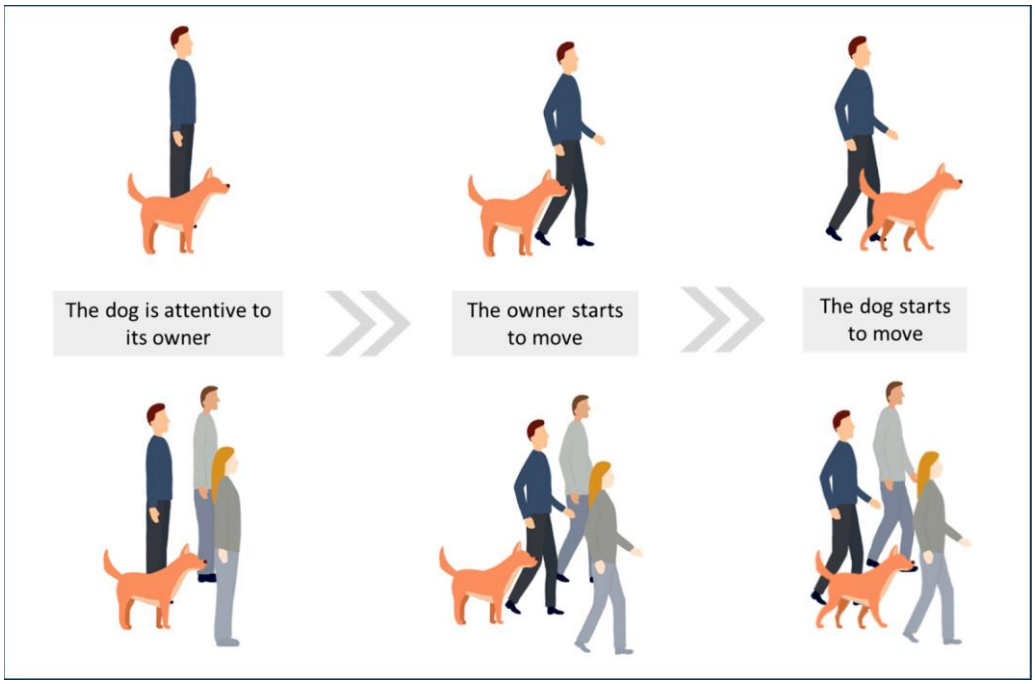


Figure 4. Interspecific locomotor synchronisation.

4.2. Motor Interference and Motor Inhibition

The perception of an action triggers the activation of representations related to that action, leading to motor resonance. Motor resonance can be demonstrated by studying the effect of action perception on the execution of another action [146–148]. Studies in humans have shown that observing an action can interfere with the simultaneous execution of another action [41,149–151]. More specifically, when a subject is instructed to perform an action while observing another individual performing the same action, the execution of the action is facilitated by motor resonance. However, if the observed action is incongruent with the performed action, this disrupts the execution of the action; this is known as motor interference [121,151]. For example, if an individual performs a hand movement in a consistent direction, either up and down or from left to right, the trajectory of the individual's hand movement is less rectilinear if the individual is observing someone else performing a gesture in the incongruent direction compared with a gesture in the same direction [151]. Similarly, when opening or closing a fist, the subject's reaction time to perform the action is delayed if the subject observes an incongruent movement compared with a congruent one [152]. In fact, the perception of the incongruent action activates the representations associated with this action simultaneously with the representations associated with the action that the subject is performing. This results in a disruption in the execution of the action due to the automatic tendency to imitate caused by the activation of mirror neurons [121]. However, subjects are still able to perform their actions, despite being influenced by the perceived action, as the automatic response triggered by motor resonance can be inhibited (see Figure 1). In other words, when observers perceive an action, they first exhibit an automatic tendency to imitate it, and then their behavioural response is to copy the action, avoid copying it, or perform a complementary action, depending on the context of the social interaction.

Thus far, motor interference and inhibition of motor resonance have only been studied in humans, and to our knowledge, there are no publications on this topic involving dogs. Studies are therefore needed to determine whether such properties are present when dogs perceive the actions of their conspecifics or humans. These studies will need to focus on actions that are part of the canine behavioural repertoire. If the perceived action is not within the observer's behavioural repertoire, sensorimotor representations associated with the action cannot be present, and consequently, motor resonance cannot occur [50].

4.3. Social Modulation of Motor Contagion

Motor contagion does not occur all the time or in all contexts. As a matter of fact, it is accentuated or inhibited by certain social modulators, such as the level of familiarity between interacting individuals, the number of social agents, attentional state, and motor experience (see [2] for a review). The social modulation of motor contagion has been the subject of numerous behavioural studies in humans. Studies have also been carried out on modulation at the interspecific level between dogs and humans. Firstly, familiarity with the model has been shown to have an effect on motor contagion and behavioural synchronisation. It is well established in humans that more affiliated individuals exhibit greater intercerebral and behavioural synchronisation compared to unfamiliar individuals [46]. The effect of familiarity is also present in dogs, whether with conspecifics or humans: motor contagion is more frequent between familiar dogs than between unfamiliar dogs [3,153]. Studies at the interspecific level have shown that pet dogs synchronise more with their owners than shelter dogs do with their caregivers [29,31], and the relationship between pet dogs and their owners is usually stronger than that between shelter dogs and their caregivers. Behavioural synchronisation thus acts as a social glue, strengthening bonds between familiar individuals [154]. Another study found that dogs exhibit a social preference for unknown humans who synchronise with them, which is further proof that behavioural synchronisation acts as a social glue at the intraspecific and interspecific levels [155]. Another social modulator of motor contagion is the number of individuals involved in the interaction. In humans, as the number of individuals increases, motor resonance becomes stronger, resulting in more pronounced behavioural synchronisation [47,156–158]. Observing multiple agents thus further activates motor representations associated with the perceived action [47]. In the context of dog–human interactions, a study investigated the effect of the number of humans on dogs' locomotor synchronisation with humans [32]. The results indicated that the level of dogs' synchronisation with their owner was equivalent, whether the owner was alone or with two other people. However, dogs' visual attention towards humans increased when the humans were in a group compared to when the owner was alone. We note that the number of people in the group may not have been sufficient to observe an effect on the dogs' locomotor synchronisation. Further studies are therefore needed to explore the effect of the number of humans more comprehensively.

Locomotor synchronisation in humans is modulated by the number of individuals but also by their locomotor profile [159]. Specifically, an individual's movement speed profile modulates the degree of behavioural synchronisation [159]. Individuals with different speed profiles synchronise less than individuals with similar speed profiles, but they still adapt to each other to synchronise [160]. A study explored the impact of locomotor profiles on dogs' locomotor synchronisation with humans by investigating dogs' locomotor synchronisation with children [161]. Children have an immature locomotor pattern [162], yet the study showed that dogs were capable of synchronising with children's locomotion. This research could be further developed by studying the effect of other human locomotor patterns on dogs' locomotor synchronisation, such as the locomotion of elderly people. Locomotor patterns of elderly people are slowed down due to age-related decline in perceptual and locomotor abilities [162]. This research would provide a better understanding of how human locomotion influences dogs' perception and motor response.

Another modulator of motor contagion in humans is motor experience [163]. As the individual's level of expertise increases, motor resonance and consequently behavioural

synchronisation become stronger [89]. This arises from the fact that visual and motor representations of action become linked through the observation and execution of the same action [164,165]. Studies have shown that brain activity during the perception of an action is higher in humans with experience in that action than in individuals with no expertise in the action [166,167]. Motor experience is acquired very early in humans, as babies just a few weeks old are already capable of behavioural synchronisation with adults [168]. Behavioural synchronisation also occurs very early in dogs, as a study demonstrated that one- and two-month-old puppies are able to synchronise with an adult person, whether familiar or not [169]. Further studies are needed to establish the effect of expertise on adult dogs' behavioural synchronisation with humans.

Other social modulators of behavioural synchronisation, such as the spatial configuration of individuals and the level of attention, have not yet been studied in dogs, leaving room for future research to substantiate the social modulation of interspecific behavioural synchronisation.

5. Conclusions

Dogs are widely acknowledged to exhibit behavioural synchronisation with humans. Behavioural synchronisation in humans is based on motor resonance and the activation of mirror neurons. The literature reveals that, given dogs' social cognitive abilities, they possess the prerequisites for motor resonance. Despite the absence of neurophysiological studies on the neural substrate of behavioural synchronisation in dogs, research on other species suggests that a mirror neuron system may exist in all social mammals. Neurological studies on dogs would confirm the existence of mirror neurons in dogs, providing direct evidence for the existence of interspecific motor resonance. Motor resonance leads to motor contagion, which can be modulated by various social factors. Behavioural studies indicate that motor contagion and its social modulation in humans are also present in dogs, thus reinforcing the hypothesis of interspecific motor resonance. However, in light of these behavioural studies, it could also be assumed that dogs' behavioural synchronisation with humans is based on an associative learning mechanism. Additional studies are therefore necessary to determine whether the properties of motor resonance, notably motor interference, are present in dog–human interactions. This review thus paves the way for future behavioural and neurophysiological research to confirm whether interspecific motor resonance underlies dogs' behavioural synchronisation with humans.

Author Contributions: A.L. drafted the article, and F.G. substantively revised it. All authors have read and agreed to the published version of the manuscript.

Funding: This work was funded by the French National Association for Research and Technology (ANRT), the association *Agir pour la Vie Animale* (AVA), the French National Centre for Scientific Research (CNRS), and Aix-Marseille University.

Institutional Review Board Statement: Not applicable.

Informed Consent Statement: Not applicable.

Data Availability Statement: No new data were created or analysed in this study. Data sharing is not applicable to this article.

Conflicts of Interest: The authors declare no conflicts of interest.

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1.3. Méthodologies employées

1.3.1. Recrutement des participants

Le chien est le deuxième animal de compagnie le plus présent en France (FEDIAF annual report, 2022.). Dans les sociétés occidentales, il est impossible de ne pas croiser de chiens au quotidien, dans les lieux privés mais aussi dans la rue ou d'autres espaces publics. Ces interactions ne sont pas toujours positives, et peuvent mener à des risques de morsures si les chiens sont dans des situations générant des manifestations de stress ou de peur (Flint et al., 2017). Compte tenu de l'omniprésence canine en France, ainsi que du risque de morsures, il est crucial de caractériser les interactions entre le chien et l'humain, pour mieux les gérer au quotidien. Pour être en mesure d'étudier ces interactions, il est essentiel de se placer dans un contexte écologique, avec des échantillons représentatifs de la population canine. C'est pourquoi dans cette thèse, tous les chiens recrutés étaient des chiens de compagnie, vivant quotidiennement avec leurs maîtres, qui les amenaient sur les sites d'expériences et repartaient avec eux à l'issue de la participation. Aucun chien n'a participé à plusieurs expériences et au total, 152 chiens adultes ont été inclus dans les études de cette thèse. Les chiens étaient tous adultes (minimum 1 an et jusqu'à 10 ans), sans problème de santé, et nous avons veillé à toujours respecter le ratio mâles/femelles dans nos études. Aucune restriction de race n'a été imposée, mis à part les races naines dont le poids était insuffisant pour les inclure dans les expériences en extérieur (voir en fin de section), car ce critère n'était pas d'intérêt pour nos recherches, d'autant plus que les études antérieures sur la synchronisation comportementale entre chiens et humains n'ont révélé que des différences mineures entre les races (Duranton & Gaunet, 2018). Cette approche nous a permis de représenter, dans la mesure du possible, la population des chiens de compagnie en France métropolitaine.

Les propriétaires étaient recrutés sur la base du volontariat et signaient un formulaire de consentement lors de leur participation. Nous n'avons pas eu besoin de faire une demande d'autorisation auprès du comité d'éthique d'Aix-Marseille Université pour les études menées au cours de la thèse, puisqu'elles étaient non invasives et sans impact sur le bien-être des chiens. L'étude présentée au Chapitre 4 a été conduite au club canin d'Agility du Gier (près de Saint-Etienne), une autorisation d'utilisation des lieux a été obtenue au préalable auprès du conseil d'administration du club canin. Les participants de cette étude étaient des adhérents du club canin. Concernant le recrutement des autres études, j'ai disposé des affiches d'appel à participation dans les parcs canins aux alentours du site des expériences, et publié des annonces sur les réseaux sociaux, permettant ainsi aux personnes intéressées de me contacter directement. La sélection des participants se faisait ensuite par téléphone, car certains critères devaient être respectés. Premièrement, les chiens devaient être à l'aise avec des personnes inconnues, pour éviter que la participation à l'étude soit génératrice de stress. Ensuite, en ce qui concerne les études en extérieur, les protocoles impliquaient que les chiens soient sans laisse, ils devaient donc avoir un rappel efficace au cas où ils s'éloigneraient trop loin. De plus, les chiens devaient peser plus de 7kg pour ne pas être gênés par le matériel utilisé (voir section 1. 3.2). Enfin,

pour l'étude présentée au Chapitre 5, portant sur l'interférence motrice, la méthodologie de l'étude imposait un haut niveau d'éducation, car les chiens devaient être capables d'apprendre une tâche précise en quelques séances. Les chiens inclus dans cette étude étaient donc habitués à participer régulièrement à des cours en club canin. Pour les autres études, aucun critère strict d'éducation n'était imposé, à l'exception du rappel. Cependant, les chiens de l'étude présentée au Chapitre 4, qui suivaient entre une fois par semaine et une fois par mois des cours d'éducation, d'agility ou de dog dancing au club d'Agility du Gier avec leurs propriétaires, avaient par conséquent un niveau d'éducation plus élevé que les commandes classiquement apprises (assis, couché, donner la patte et rappel).

1.3.2. Méthodes pour investiguer les modulateurs sociaux de la synchronisation comportementale chez le chien

1.3.2.1. Sélection du contexte expérimental et des sites d'étude

Nous avons choisi d'utiliser le contexte de la marche pour étudier la modulation sociale de la synchronisation comportementale chez le chien, car cette forme d'alignement comportemental survient spontanément lorsque les individus marchent ensemble (Katevas et al., 2015). De plus, marcher ensemble est un comportement ancestral partagé par les chiens et les humains depuis des millénaires (Bergström et al., 2020). Les expériences de la thèse ont été menées dans des environnements extérieurs, sans laisse, afin que les chiens puissent se déplacer librement, sans être contraints physiquement, ni être dans l'attente d'une commande humaine. Cette approche permet ainsi d'observer le comportement spontané des chiens de compagnie envers l'humain.

Les études portant sur l'effet de la synchronisation d'une personne inconnue sur le chien, ou sur son propriétaire et l'effet du nombre de personnes ont été réalisées dans un espace public ouvert, à proximité de Toulouse (Figure 2. A.). Ce site, caractérisé par une vaste superficie et un faible passage, offrait un cadre écologique idéal pour la collecte de données : il était comparable à n'importe quel lieu de promenade, sans perturbation causée par la présence d'autres personnes.

L'étude portant sur l'effet du type d'agent social a été menée dans un parc clos au sein du club canin d'Agility du Gier (Figure 2. B.). Nous avions choisi cet environnement car notre but initial était de comparer la synchronisation comportementale entre deux chiens avec la synchronisation comportementale entre un chien et un humain, en l'absence d'autres individus. Il était donc nécessaire que les deux chiens soient dans un environnement fermé pour éviter qu'ils puissent s'échapper en l'absence de surveillance humaine. Cependant, lorsque nous avons testé ce protocole, nous avons constaté que, sans la présence humaine dans le parc, les chiens avaient tendance à rester près de la porte de sortie et interagissaient très peu. Nous avons donc modifié le protocole, en incluant la présence des propriétaires dans la zone d'observation, ce qui a effectivement, et c'est intéressant en soi, conduit à une augmentation des interactions entre les chiens.

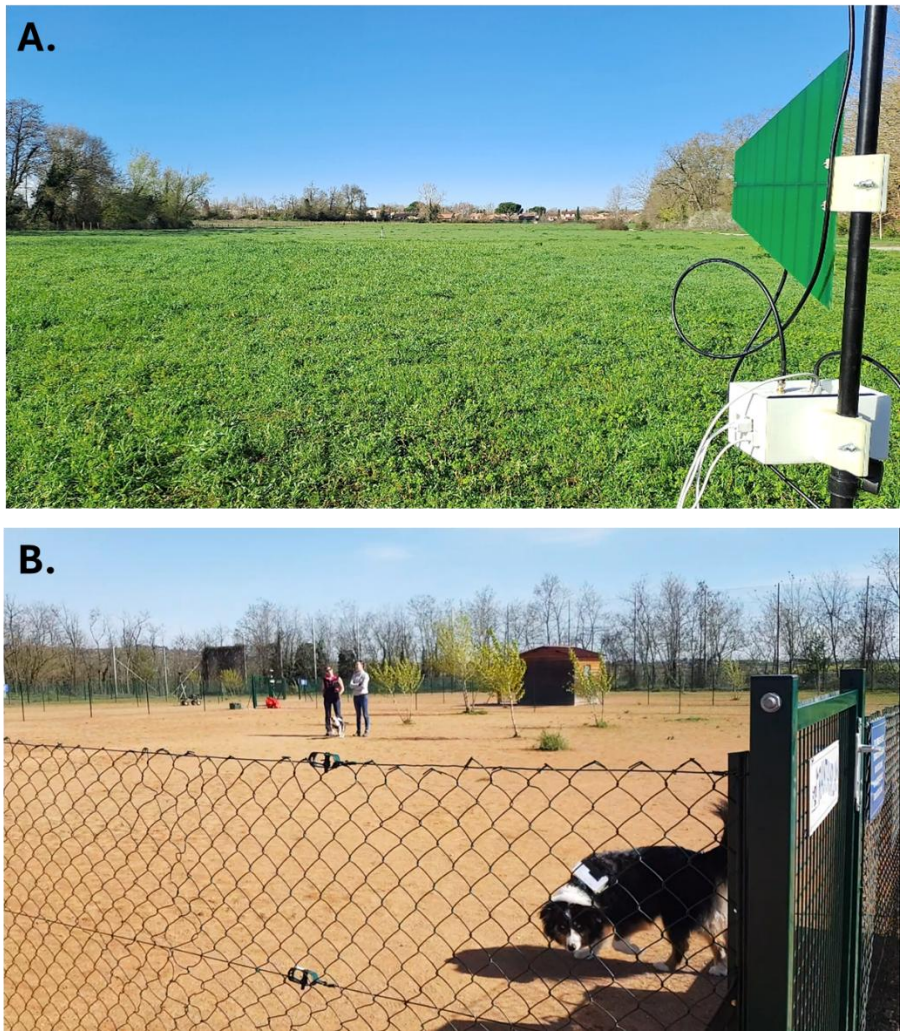


Figure 2. Sites expérimentaux **(A)** à proximité de Toulouse et **(B)** au sein du club canin d'Agility du Gier.

1.3.2.2. Mesure de la synchronisation locomotrice (temporelle, d'activité et de localisation) à l'aide de la technologie RTK

Pour mesurer la synchronisation comportementale, nous avons utilisé les trois composantes définies par Duranton et Gaunet (2016), à savoir la synchronisation de localisation (être au même endroit au même instant), la synchronisation d'activité (produire le même comportement au même instant), et la synchronisation temporelle (changer de comportement en même temps). Dans le contexte de la marche, c'est en fait la synchronisation locomotrice que nous avons mesurée. Pour ce faire, il fallait relever les positions des participants au cours du temps afin de calculer la distance entre eux (synchronisation de localisation), leur vitesse respective (synchronisation d'activité) et leurs changements de vitesse (synchronisation temporelle). Les données de position peuvent être obtenues à partir d'enregistrements vidéo en utilisant la technique de triangulation, avec des caméras calibrées et positionnées à différents endroits pour déterminer la position des points d'intérêt, dans notre cas des participants (Houssineau et al., 2016). Néanmoins, cette méthode exige une calibration parfaite, nous avons donc envisagé d'autres outils de mesure. Nous avons considéré l'utilisation de drones pour filmer la zone expérimentale par le dessus, avec l'axe de la caméra perpendiculaire au sol. Cependant, la législation sur l'utilisation des drones en France s'est renforcée en 2021, limitant grandement les zones de vol autorisées (Vacher, 2022). De plus, les drones peuvent être bruyants, ce qui aurait pu interférer avec le comportement spontané des chiens. Nous avons finalement opté pour l'utilisation de GPS (Global Positioning System), une technologie couramment employée pour collecter des données de mouvement (Hebblewhite & Haydon, 2010). Avec ce système, un satellite envoie un signal au récepteur GPS, le temps mis pour recevoir ce signal permet de calculer la distance séparant le récepteur du satellite. Cette distance est calculée pour au moins 4 satellites, la position du récepteur est ainsi déterminée par triangulation de ces distances. Néanmoins, la précision des GPS classiques est de l'ordre du mètre, ce qui n'est pas satisfaisant dans notre contexte expérimental. La solution est d'utiliser la technologie RTK (Real Time Kinematic) (Feng & Wang, 2008). Cette technique nécessite une station de référence fixe (Figure 3. A), dont la position exacte est connue, qui envoie via une antenne hertzienne des corrections en temps réel aux récepteurs GPS mobiles portés par les participants (Figure 3. B.). Les récepteurs étaient donc équipés d'une antenne GPS pour le calcul de la position et d'une antenne hertzienne pour recevoir les corrections RTK. Ces corrections étaient intégrées en temps réel dans le calcul de la position des récepteurs, permettant une précision centimétrique (Feng & Wang, 2008). La fréquence des données de position était de 4 Hz. Pour les besoins de la thèse, ce matériel (une station de référence et 7 récepteurs mobiles) a été acheté auprès de la société e-Whiz®, basée à Auzielle (31650). En complément des GPS, nous avons utilisé trois caméras, deux sur trépied et une Go-Pro © attachée sur le harnais des chiens (Figure 3. C.), pour enregistrer leur comportement, principalement leur activité de regard.



Figure 3. Matériel utilisé pour mesurer la synchronisation locomotrice. **(A)** La station de référence, dont la position exacte est connue, envoie des corrections aux récepteurs mobiles par une antenne hertzienne (antenne verte sur la photographie). **(B)** Chaque participant portait un récepteur GPS qui recevait les corrections de la station de référence. Les antennes GPS des récepteurs étaient fixées sur des casquettes pour les récepteurs destinés aux humains, tandis qu'elles étaient intégrées directement dans le boîtier pour les récepteurs destinés aux chiens. **(C)** Les chiens portaient un harnais sur lequel était fixé le boitier GPS et une caméra Go-Pro ©.

1.3.3. Méthodes pour investiguer la résonance motrice interspécifique

La dernière expérience, présentée au Chapitre 5, avait pour objectif d'explorer l'interférence motrice, une propriété de la résonance motrice, au niveau interspécifique, ce qui n'avait jamais été fait auparavant. L'interférence motrice se produit lorsque l'exécution d'une action est perturbée par l'observation simultanée d'une action incongruente (Cracco et al., 2018). Pour tester l'interférence motrice chez le chien lors de l'observation d'un comportement humain, il était nécessaire de sélectionner une action – ainsi que l'action incongruente correspondante – présentes dans le répertoire comportemental des deux espèces. Nous avons d'abord envisagé des comportements tels que se lever/s'asseoir, ou se mettre en mouvement/s'arrêter. Ces comportements auraient permis de maintenir une continuité méthodologique avec les études sur la marche. Cependant, leur exécution chez le chien est fortement dépendante de l'apprentissage. Par exemple, certains chiens ont appris à s'arrêter sur commande, que leur propriétaire s'arrête ou continue de marcher, tandis que d'autres s'arrêtent

uniquement lorsque leur propriétaire s'arrête. Par conséquent, il était crucial de choisir une action qui n'était pas déjà apprise avant l'expérience.

En nous appuyant sur les études de l'interférence motrice chez l'humain, nous avons choisi l'action de poser la patte sur une partie spécifique d'un support, ce dernier ayant été conçu spécialement pour l'expérience (Figure 4). L'action incongruente de l'humain était de poser la main à une hauteur différente par rapport à celle apprise par le chien. L'expérience comportait une phase d'apprentissage, répartie sur plusieurs séances, au cours desquelles j'apprenais aux chiens à réaliser l'action cible en réponse à un signal sonore. Ce dernier était émis par un boîtier central lorsque j'appuyais sur le bouton fixé sur la poignée (Figure 4). Cette expérience se déroulait au domicile des propriétaires, tous résidant à Toulouse ou dans ses environs, afin de limiter les distractions pour les chiens. La phase d'apprentissage contrôlée garantissait une uniformité dans la manière dont les chiens ont appris l'action cible. Toutefois, cela a imposé le critère de sélection concernant le niveau d'éducation des chiens : ils devaient être habitués à régulièrement travailler et être capables d'atteindre un haut niveau de performance en quelques séances (plus de 80 % de réussite, soit exécuter l'action suite à l'émission du signal sonore au moins 10 fois sur 12).

Le support était équipé d'un système capacitif qui enregistrait le temps écoulé entre l'émission du signal sonore et le contact avec l'une des touches. Ce système permettait, pour la phase de test, de comparer le temps de réaction des chiens pour réaliser leur action en fonction des actions que j'exécutais simultanément au signal sonore (l'exemple présenté en Figure 4 illustre une action congruente). Un algorithme programmé sur un Arduino indiquait de façon aléatoire le type d'action que je devais effectuer, lequel s'affichait sur l'écran du boitier central.

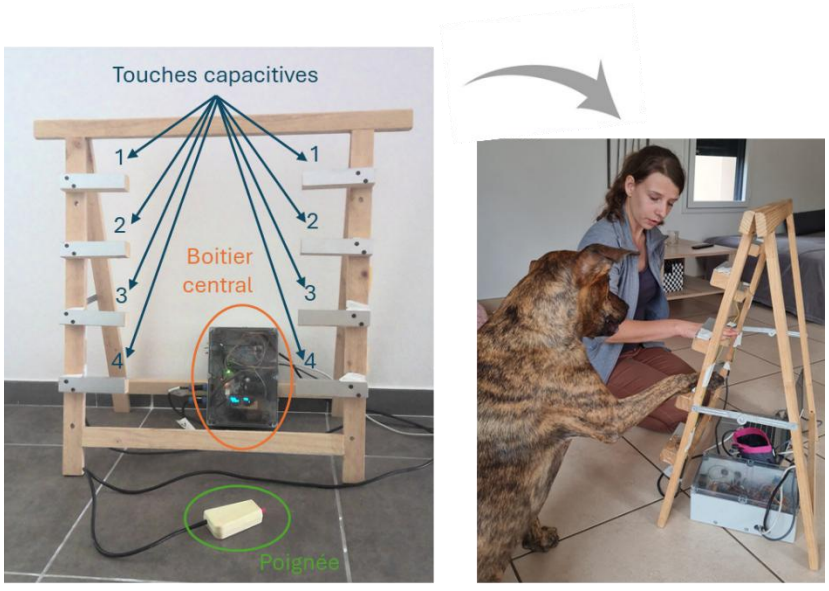


Figure 4. Matériel utilisé pour l'étude portant sur l'interférence motrice interspécifique. A droite, un exemple avec une action humaine congruente effectuée lors de l'émission du signal sonore.

2. Modulation de la synchronisation comportementale chez le chien par le comportement d'une personne inconnue

2.1. La synchronisation de la marche d'une personne inconnue sur celle du chien augmente ultérieurement la synchronisation du chien sur la personne

Le premier modulateur social de la synchronisation comportementale que nous avons étudié est l'effet du comportement d'une personne non familière sur la synchronisation locomotrice des chiens envers cette personne. Les précédentes recherches ont mis en évidence la synchronisation comportementale entre des chiens et des personnes familières (Duranton et al., 2017, 2019b). Une seule étude a porté sur la synchronisation interspécifique en impliquant des humains non familiers des chiens, montrant que ces derniers préféraient aller vers une personne inconnue qui s'est synchronisée sur eux plutôt qu'une personne qui ne l'avait pas fait (Duranton et al., 2019a). Compte tenu de l'importance de comprendre la synchronisation comportementale entre les chiens et les personnes non familières — les chiens étant régulièrement confrontés à des inconnus au quotidien—nous avons approfondi cette question. Nous avons ainsi investigué si les chiens se synchronisent davantage avec une personne non familière qui serait d'abord synchronisée sur eux. En d'autres termes, est-ce que la synchronisation d'une personne inconnue sur un chien induit en retour la synchronisation du chien avec cette personne ? Sur la base de la littérature existante, nous avons émis l'hypothèse que les chiens montreraient effectivement une synchronisation locomotrice plus prononcée avec une personne si celle-ci s'était préalablement synchronisée sur eux.

Pour cette expérience, réalisée en présence des propriétaires mais qui restaient neutres et statiques, deux groupes expérimentaux ont été comparés et je jouais le rôle de la personne inconnue. Pour le premier groupe de chiens, j'ai synchronisé ma locomotion sur celle des chiens pendant 15 minutes, tandis que pour le second groupe, j'ai désynchronisé ma locomotion de celle des chiens pendant la même durée. Ensuite, grâce aux relevés GPS pendant que je marchais à différentes allures, en ligne droite, pendant 45s, la synchronisation temporelle, d'activité et de localisation des chiens sur ma propre locomotion a été caractérisée.

Les résultats indiquent une plus forte synchronisation locomotrice des chiens du premier groupe expérimental pendant la marche en ligne droite par rapport à ceux du

second groupe. Il est important de noter que cet effet était temporaire, car les chiens avaient tendance à revenir vers leur propriétaire avant la fin de la marche en ligne droite.

Ces résultats suggèrent que la synchronisation comportementale peut se propager : la synchronisation locomotrice d'une personne sur un chien entraine la synchronisation locomotrice du chien sur la personne en retour. De plus, comme les chiens se synchronisent habituellement sur les personnes familières, nos résultats offrent un apport pratique non négligeable, en montrant que s'ajuster aux mouvements d'un chien inconnu peut aider à se familiariser avec lui. Enfin, cette étude souligne l'importance des propriétaires, qui agissent comme des attracteurs sociaux pour les chiens.

Article 2 : Lamontagne, A., Legou, T., Bedossa, T., & Gaunet, F. (2024). Walk with me? Part 1: Dogs synchronize with an unfamiliar person who first synchronized with them. *Applied Animal Behaviour Science*, *272*, 106204.

https://doi.org/10.1016/j.applanim.2024.106204

Applied Animal Behaviour Science 272 (2024) 106204



Contents lists available at ScienceDirect

Applied Animal Behaviour Science

journal homepage: www.elsevier.com/locate/applanim



Walk with me? Part 1: Dogs synchronize with an unfamiliar person who first synchronized with them

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ARTICLE INFO

Keywords:
Behaviour
Dog
Interspecific interactions
Motor contagion
Synchronization
Direct sensitivity

ABSTRACT

Dogs are sensitive to human social signals directed towards them. In this study, we investigated how this direct sensitivity affects dogs' behavioural synchronization. To do so, we compared two experimental groups: an unfamiliar person either synchronized their locomotion with that of each dog for 15 minutes for the first group (n = 16) or desynchronized their locomotion with that of each dog for 15 minutes for the second group (n = 16). We then compared the dogs' locomotor synchronization with the unfamiliar person and the dogs' gaze behaviour during a straight-line walk. Dogs were off leash throughout the entire procedure, the owner was present but neutral and static during the whole procedure, except for 9 dogs who remained inactive for too long during the 15-minute period, requiring owners to briefly intervene to re-engage them in activity. We found that dogs from the first group engaged less in social referencing towards the unfamiliar person during the 15 minutes, and synchronized more with them and tended to go to their owner later during the straight-line walk compared to dogs from the second group. We thus demonstrated that dogs, upon perceiving behavioural synchronization from an unfamiliar person, reciprocate with behavioural synchronization towards this person, thereby elucidating for the first time motor contagion at the interspecific level. Also, since dogs usually synchronize their behaviour only with familiar humans, our findings suggest that synchronizing with dogs, by maintaining a proximity of 1 m and an average speed difference of 0.2 m/s, is a way of becoming familiar with them. We thus offer a valuable tool, applicable in various daily situations in which the owner is present, to facilitate familiarization between dogs and unfamiliar people, without the need for food or direct contact with dogs.

1. Introduction

Dogs exhibit remarkable sensitivity to humans' body positions, gestures, head and hand directions (Kaminski and Nitzschner, 2013; Reid, 2009; Rooney et al., 2001; Vas et al., 2005) as well as to humans' attentional states (Gácsi et al., 2004; Kaminski and Nitzschner, 2013; Virányi et al., 2004). Human behaviour has a direct effect on dog behaviour (Vas et al., 2005), and dogs' behavioural responses also depend on their level of familiarity with humans (Duranton et al., 2017a, 2019a; Duranton and Gaunet, 2016, 2018; Kaminski and Nitzschner, 2013; Kerepesi et al., 2015; Kuhne et al., 2012). This holds particularly true for pet dogs, as shelter dogs exhibit less difference in their behavioural response towards familiar and unfamiliar people (Conley et al., 2014; Döring et al., 2014; McGuire et al., 2023). In contrast to shelter dogs, pet dogs' behaviour differs when they are with an unfamiliar person, a familiar person, or with their owner. Notably, they are more attentive to their owner than to other individuals (Horn et al., 2013), and they spend more time with their owner than with an unfamiliar person in an unfamiliar environment (Kerepesi et al., 2015). Interestingly, this effect of familiarity is context-dependent, as pet dogs allocate more time to the unfamiliar person in a familiar setting (Feuerbacher et al., 2017). Moreover, in non-play interactions with an unfamiliar person, pet dogs spend less time looking at the person and more time avoiding the latter compared to non-play interactions with their owner (Győri et al., 2010). Finally, pet dogs exhibit more soothing and contact-seeking behaviours when they are petted by a familiar person than by an unfamiliar person (Kuhne et al., 2012).

A number of studies have investigated the effect of an unfamiliar

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https://doi.org/10.1016/j.applanim.2024.106204
Received 2 January 2024; Received in revised form 16 February 2024; Accepted 18 February 2024
Available online 20 February 2024
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person's behaviour on a dog's behavioural response when encountering the person (Barrera et al., 2010; Brubaker et al., 2019; Gácsi et al., 2013; Győri et al., 2010; Jakovcevic et al., 2012; Lucidi et al., 2005; Mariti et al., 2018; Ortolani et al., 2009; Palestrini et al., 2005; Prato-Previde et al., 2003; Svartberg and Forkman, 2002; Topál et al., 1998; Valsecchi et al., 2011; Vas et al., 2005, 2008). The unfamiliar persons acted either passively or actively, in or not in the presence of the owner for studies involving pet dogs. When the unfamiliar persons were active, they exhibited either friendly behaviour (normal gait, a soft voice, petted the dog) or threatening behaviour (slow gait and direct gaze into the dog's eyes). The results of these studies converge: dogs adjusted their behaviour according to the unfamiliar person's behaviour. Dogs indeed avoided the person, looked away and vocalized if the person exhibited threatening behaviour; conversely, they were neutral or sought contact if the person exhibited friendly behaviour. When the person's behaviour changed, the dogs quickly, flexibly and consistently adapted their behavioural response. In addition, for pet dogs, their response to the unfamiliar person differed depending on the presence or absence of the owner. Specifically, when their owner was not present during the encounter, pet dogs spent less time near the unfamiliar person, sought less contact even when the unfamiliar person exhibited friendly behaviour, spent less time exploring the room and spent more time at the exit door than when their owner was present. Overall, dogs exhibited 'direct sensitivity' to human behaviour.

Dogs are also able to quickly establish a social preference for one unfamiliar person over another. In concurrent choice tests, dogs were presented with two unfamiliar people who each exhibited different behaviours; the researchers then noted which person the dog went to first and compared the time the dog spent near each person (Duranton et al., 2019b; Feuerbacher and Wynne, 2017; Gácsi et al., 2001). These studies showed that dogs established a social preference for one of the two people within 15 minutes. Moreover, their preference for the one person was similar in magnitude to the pet dogs' preference for their owner. Specifically, the amount of time spent by the dogs near the preferred person was not significantly different from the amount of time spent by pet dogs near their owner in a similar setting.

Dogs' social preference can also be affected by human behavioural synchronization (Duranton et al., 2019b). Behavioural synchronization is a form of spontaneous behavioural alignment, ubiquitous in many social species, and defined by three components: it occurs when two or more individuals exhibit the same behavioural patterns (activity synchronization) in the same space (location synchronization) and within fewer than 3 seconds (temporal synchronization) (Duranton and Gaunet, 2015). Behavioural synchronization has been mainly studied at the intraspecific level (see Lamontagne and Gaunet (2023) for a comprehensive review), and more recently at the interspecific level, as recent studies have shown that dogs synchronize their locomotor behaviour with that of their owner without any reinforcement during off-leash walks, in either an indoor or outdoor environment known or unknown to the dogs (Duranton et al., 2017b, 2018; Foltin, 2021; Lamontagne et al., 2023). In a concurrent choice test, pet dogs had a social preference for an unfamiliar person who synchronized their locomotion with the dog's compared to an unfamiliar person who did not (Duranton et al., 2019b). This choice task was carried out in the owners' homes, and only involved working breeds. However, in everyday life, pet dogs of all breeds encounter an average of 3–5 people per week (Westgarth et al., 2008), at a veterinary clinic or during walks in public spaces for instance (Duranton and Gaunet, 2015). It is therefore important to identify how the behaviour of an unfamiliar person can affect the dog's ecological behavioural response ourdoors. This holds interest at several levels. Firstly, unfamiliar people may inadvertently adopt approaches that are frightening for dogs, so understanding the behaviours they can exhibit would limit stress and enhance the emotional well-being of dogs. This knowledge can also prevent aggressive or anxious responses from dogs, thereby safeguarding unfamiliar people from potential injury. Additionally, it facilitates future encounters between dogs, their owner, and unfamiliar people, fostering positive socialization experiences. In summary, identifying these behaviours is essential for promoting the well-being of dogs, enhancing their socialization, and ensuring indi- vidual and public safety, ultimately contributing to a harmonious coexistence between humans and dogs. That is why in this study, we aimed to further understand the consequences of human behavioural synchronization with dogs on dogs' ecological behavioural responses, i.e. dogs' direct sensitivity to human behavioural synchronization, whatever the dogs' breeds. Given dogs' sensitivity to people's behaviour towards them, we hypothesized that if an unfamiliar person synchronized their locomotion with a dog's in an outdoor environment, this would result in stronger locomotor synchronization from the dog than if the unfamiliar person did not synchronize their locomotion. We therefore conducted an experiment with two experimental groups: during a first phase, an unfamiliar person synchronized their locomotion with that of the dogs for one group (the synchronization with dog locomotion (Sync) group); for the other group, the unfamiliar person desynchronized their locomotion with that of the dogs (the desynchronization with dog locomotion (Desync) group). We analyzed the dogs' visual and olfactory attention when the unfamiliar person synchronized or desynchronized their locomotion with the dog's during this first phase. We next compared the dogs' locomotor synchronization with the unfamiliar person during a straight-line walk (second phase). Based on the aforementioned studies, we hypothesized that the dog's locomotor synchronization with the unfamiliar person would be stronger for dogs in the Sync group than for dogs in the Desync group, resulting in a shorter distance between the dog and the person and more time spent near the person (location synchronization); a smaller difference between the dog's speed and the person's speed and more time spent at a similar speed (activity synchronization); and a greater number of dogs who adjust their speed when the person changed their speed (temporal synchronization) for dogs in the Sync group compared to dogs in the Desync group. We also compared gazing behaviour between the two experimental groups and hypothesized that dogs in the Sync group would spend more time gazing at the person and less time gazing at their owner than dogs in the Desync group.

2. Material and methods

2.1. Ethical note

This experimental study was conducted in accordance with the Declaration of Helsinki and its latest revision in 2013, the legal requirements of France and the institutional guidelines of Aix-Marseille University. The ethics committee stated that this study was exempt from ethical approval because it was conducted in an unrestricted outdoor environment without any physical constraints for the dogs. All owners who participated signed a consent form. All the dogs were in good health, and none showed signs of aging or behavioural problems, based on information from the owners and observations by the experimenter (a veterinarian). All the dogs were used to humans and were not fearful of unfamiliar people. They were all used to being walked off leash and wearing a harness. No physical restraint was imposed on the dogs during the experiment. The dogs wore a Gopro® harness with a GPS and a Gopro® camera attached to it during the experiment, and they were given 10 minutes to get used to wearing the harness. During the experiment, none of the dogs exhibited any stress or fear signals. At the end of the experiment, all the dogs returned home with their owners.

2.2. Participants

Thirty-two dogs with a minimum weight of 7 kg and from any breed or crossbreed (dog breeds are presented in Table 1 in the Supplemental File 1) participated. Sample size was calculated beforehand on the basis of previous research using a similar protocol (Duranton et al., 2018; Lamontagne et al., 2023). Dogs' breeds were assigned based on

information provided by owners when available, and visual inspection otherwise. We acknowledge that visual inspection may not be as reliable as DNA analysis, but in our study, breed identification was for descriptive purposes only and not included as a factor in our analyses. Half of the dogs, counterbalanced for sex, were assigned to an experimental group with the unfamiliar person synchronizing their locomotion to that of the dog for 15 minutes (Sync group). The other half of the dogs, counterbalanced for sex, were assigned to an experimental group with the unfamiliar person desynchronizing their locomotion to that of the dog for 15 minutes (Desync group). The dogs were 1–9 years old (mean $\pm$ *SD* = 3.43 $\pm$ 1.90 years old; mean $\pm$ *SD* for dogs in the Sync group = 2.60 $\pm$ 1.07 years old; mean $\pm$ *SD* for dogs in the Desync group = 4.25 $\pm$ 2.20 years old). All dogs knew basic training commands (sit, down, come). Out of the 32 dogs, 25 were neutered, and 7 were intact (2 females in the Desync group, 3 females in the Sync group, 1 male in the Desync group, and 1 male in the Sync group).

2.3. Experimental procedure

Dogs were tested individually in an open outdoor space near Toulouse, France. The test site was identical for all dogs and consisted of an open area of grass, approximately 100 m by 200 m, totaling 20 000 m^2, ensuring unrestricted movement for the dogs (Supplemental File 2). Data were collected over a period of 2 months. It was possible to test two dogs on the same day, with several hours between each test. Situated in a public area, the test site was accessible to humans, pets, and other animals, although traffic was minimal. Tests were conducted on weekdays during periods of very low traffic to ensure that our observations would not be disrupted by the presence of other individuals or animals. We did not experience any disturbances during the tests. The owner was present during the test; no other individuals were present. The dog was off leash and no instruction was given to the dog during the entire experimental procedure. Data were recorded with a Real Time Kinematic positioning (RTK) technique which uses a base station (Supplemental File 2) that sends real-time corrections to Global Positioning System (GPS) devices to achieve centimetric precision. The same experimenter played the role of the unfamiliar person for all the dogs. The experimenter and the dog wore a GPS device on their back. Each device recorded the time, location and the quality of the RTK correction every 0.25 seconds. The processing of the GPS data provided 4 data per second for the distance between the two GPS devices, and 4 data per second for the speed of each GPS.

When the owner and dog arrived at the test site, the owner attached a harness with a GPS and a GoPro® camera on their dog's back. The dog was then given 10 minutes to get used to the equipment and freely explore the test site. During this time, the experimenter equipped themselves with a harness with a GPS and briefly explained the experimental procedure to the owner. The owner then went to the side of the test site and stayed there, in full view of the dog, until the experimental procedure was completed. The experimenter and the owner each displayed a neutral facial expression during the whole experiment. The experiment took place in two phases:

2.3.1. Phase 1: 15 min of synchronization or desynchronization with dog locomotion (Fig. 1.A and Supplemental File 3)

When the dog had finished exploring, the experimenter called the dog to join them, turned on the 2 GPS devices and then observed the dog in one of the two experimental groups: for the synchronization with dog locomotion (Sync) group, the experimenter synchronized their locomotion with that of the dog for 15 minutes: they stayed close to the dog and adjusted their speed to that of the dog; for the desynchronization with dog locomotion (Desync) group, the experimenter desynchronized their locomotion with that of the dog for 15 minutes: they stayed away from the dog and did not adjust their speed to that of the dog.

We aimed to have no visual cues from the experimenter and to minimize their verbal cues during this phase, so that the dog's behavioural response could be attributed as much as possible to the experimenter's locomotor behaviour. In both experimental groups, the experimenter thus filmed the dog with a hand-held camera, and did not look directly at the dog but observed the dog through the camera's feed. The owner did not look at or talk to the dog. If the dog did not look at the experimenter for 1 minute, they called the dog's name. The aim was to keep the dog's attention focused on the experimenter. Additionally, since the owner remained inactive during the experimental procedure, and dogs tend to synchronize with their owners, we established rules to prevent the dogs from remaining inactive for extended periods. If the dog was inactive for 1 minute, the experimenter called the dog's name. If the dog was still inactive after 2 minutes, the experimenter indicated to the owner with a discreet wave for the owner to say the dog's name. If the dog was still inactive after 3 minutes, the experimenter discreetly signalled to the owner to walk a few steps. The aim was to keep the dog active during the experiment, since dogs are accustomed to keeping an eye on their owner.

2.3.2. Phase 2: 45 s straight-line walk (Fig. 1.B and Supplemental File 3)

After the 15-minute phase of synchronization or desynchronization of the experimenter with the dog's locomotion, owners returned to their initial position if necessary and remained there until the end of the test. The experimenter then turned on the Gopro® camera attached to the dog's harness and two cameras installed on tripods, then they went to the starting point of the straight-line walk and called the dog to them. They faced Camera 1 and the experimenter used their phone as a timer. When they started the timer, an initial countdown of ten seconds began, they could look at or talk to the dog during this time. After the countdown, the experimenter stopped communicating with the dog, turned 180° and walked in a straight line in the three speed conditions (static, slow walk and fast walk) in a randomly assigned order without a break between them. A beep was emitted every 15 seconds by the application to notify the experimenter to change speed. Beeps were emitted over the experimenter's headphones so as not to distract the dog. The order of the speed conditions was randomly assigned for each dog. In the static condition, the experimenter stayed still for 15 seconds. In the slow-walk condition, the experimenter walked slowly in a straight line for 15 seconds. In the fast-walk condition, the experimenter walked quickly in a straight line for 15 seconds. Neither the experimenter nor the owner looked at or talked to the dog during the straight-line walk. Fig. 1.

2.4. Data analysis

2.4.1. Phase 1

During Phase 1, we first checked that the mean distance and the mean absolute difference between the dog's speed and the experimenter's speed were smaller for dogs in the Sync group compared to dogs in the Desync group. This would confirm that the experimenter correctly synchronized and desynchronized with the dogs' locomotion.

We next conducted exploratory analyses of the dogs' behaviour on the following variables using video recordings: gaze at the experimenter, proximity to the owner, visual attention to an element other than the experimenter, olfactive attention, and motor inactivity. The definition of each of these variables is provided in Table 1. To analyze dogs' behavioural responses, we performed analyses of variance (ANOVA) in R (version 4.2.1, https://www.r-project.org) with experimental group (2 levels: synchronization with dog locomotion (Sync) and desynchronization with dog locomotion (Desync)) as a between-subject factor and the dog's sex (2 levels: male and female) and age (2 levels: young adult, i.e. between 1 and 2 years old, and mature adult, i.e. over 2 years old, based on the classification proposed by Harvey (2021)) as control predictors.

2.4.2. Phase 2

During Phase 2, we analyzed dogs' locomotor synchronization with the experimenter, gazing behaviour, and social attraction to their owner. The definition of each of the dependent variables is provided in Table 2.

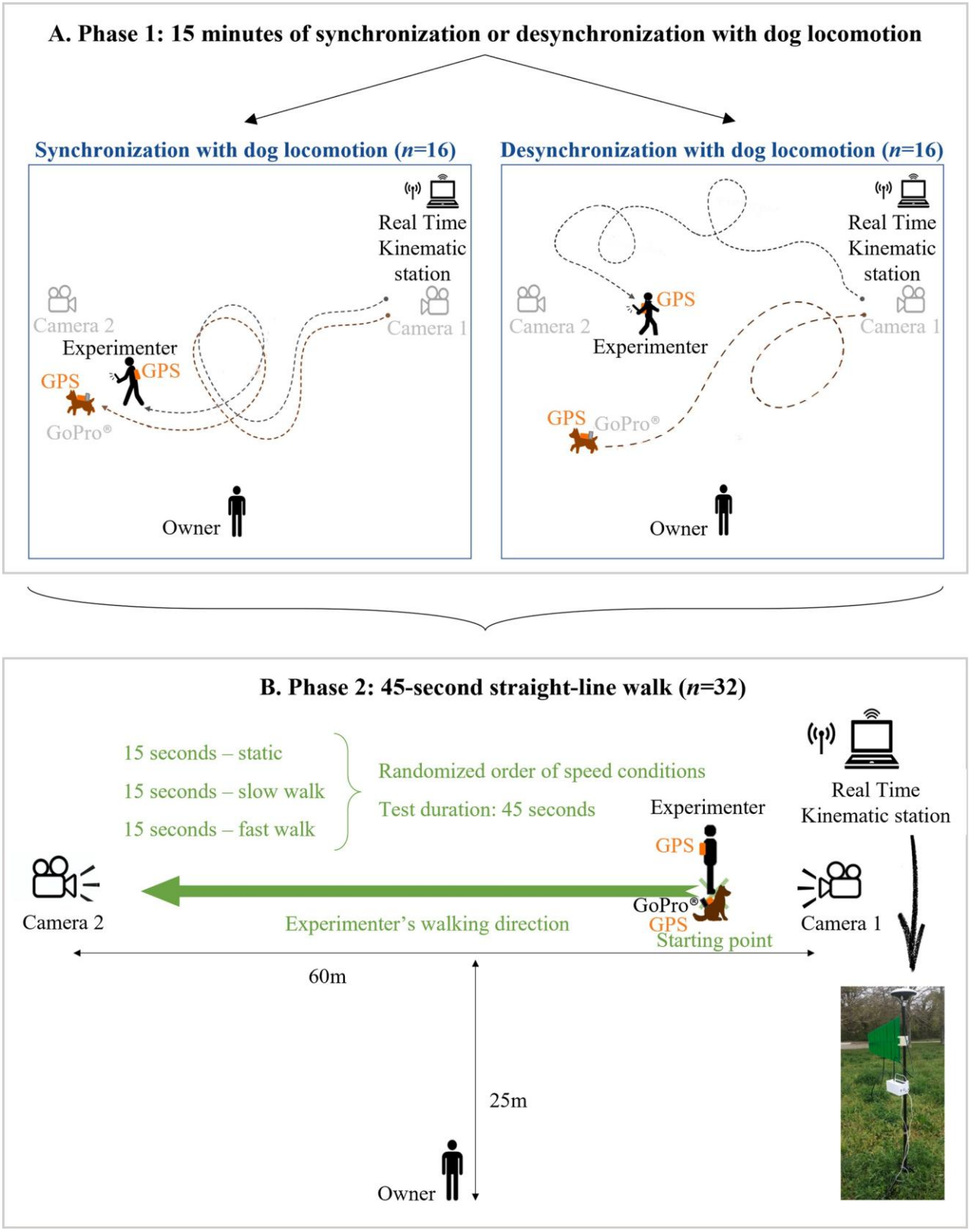


Fig. 1. Experimental procedure. A. Each dog was assigned to one of the two experimental groups. B. After 15 minutes of synchronizing or desynchronizing with the dog's locomotion, the experimenter walked in a straight line at three different speeds.

Table 1
Definitions of the dependent variables studied in Phase 1.

Dependent variable	Definition
Gaze towards experimenter	Time in seconds spent with the dog's nose oriented towards the camera held by the experimenter.
Proximity to owner	Time that the dog spent at the owner's feet, which were therefore visible in the camera's field.
Visual attention to elements other than experimenter	Time in seconds that the dog spent static, with body in tension, head straight and gaze fixed and not directed towards the experimenter.
Olfactive attention	Time in seconds that the dog spent motionless or moving very slowly and with muzzle on the ground.
Motor inactivity	Time in seconds that the dog spent sitting or lying down, without engaging in visual, olfactory or auditory attention.

To investigate location synchronization (Table 2), we analyzed the distance between the dog and the experimenter, and the time the dog spent within 5 m of the experimenter. We chose this threshold because a previous study using the same straight-line walk protocol showed that dogs stay on average 5 m away from their owner (Lamontagne et al., 2023). To study activity synchronization (Table 2), we analyzed the difference between the dog's speed and the experimenter's speed, keeping in mind that the Lamontagne et al. study showed that the average speed difference between dogs and owners in an off-leash situation was 0.04 m/s. We performed linear mixed effects models (LMM) in R with the lme4 package (Bates et al., 2015) to analyze location synchronization and activity synchronization. We included dog participants as random effects. The following independent variables were included as fixed effects, as well as the interaction between these variables: experimental group (2 levels: synchronization with dog locomotion (Sync) and desynchronization with dog locomotion (Desync)), speed condition (3 levels: static, slow walk, fast walk) and period in the straight-line walk (3 levels: first period = the first 15 seconds of the test, second period = the following 15 seconds, third period = the last 15 seconds of the test). For our models of distance and speed difference, as data were collected every 0.25 seconds, we included an autocorrelation structure of order 1. We included the dog's sex (2 levels: male and female) and age (2 levels: young adult and mature adult) as control predictors. We did not consider their significance since the role of control predictors is not to test for the effect of these control predictors but only to control for them in LMMs. The possible effects of control predictors may be endogenous, so it is unlikely that these predictors themselves have a causal interpretation (Hünermund and Louw, 2020).

To explore temporal synchronization (Table 2), we analyzed the dog's latency. We considered that the dog presented a latency when the following criteria were met: the presence of a slope on the speed graph obtained from GPS data and a change in gait based on a qualitative analysis of the camera recordings. Three gaits were taken into account: walking, trotting and galloping. We used a chi-square test to compare the proportion of dogs that exhibited a latency within the two experimental groups. We then performed a LMM on dogs that showed latencies, and we included dog participants as random effects, experimental group as a between-subject factor and the dog's sex and age as control predictors.

We also analyzed dogs' gazing behaviour towards the experimenter and towards the owner using LMMs. We included dog participants as random effects, and the experimental group, speed condition and straight-line walk period as fixed effects, as well as the interaction between these variables. We included the dog's sex and age as control predictors.

Finally, as previous studies have shown that owners are social

Table 2
Definitions of the dependent variables studied in Phase 2 and associated independent variables.

	Dependent variable	Definition	Independent variables
Location synchronization	Distance between dog and experimenter	Distance in metres between the experimenter's back and the middle of the dog's back. Calculated every 0.25 seconds from GPS data. 179 values per dogs	Experimental group Speed condition Straight-line walk period
	Time spent near experimenter	From GPS data, time in seconds during which the distance between the 2 GPS was less than 5 m. Three values per dog calculated from GPS data.	Experimental group Speed condition Straight-line walk period
Activity synchronization	Speed difference	Absolute difference in metres per second between the experimenter's speed and the dog's speed. Calculated every 0.25 seconds from GPS data. 179 values per dogs	Experimental group Speed condition Straight-line walk period
	Time spent at similar speed	Time in seconds during which the speed difference was less than 0.5 m per second. Three values per dog, calculated from GPS data.	Experimental group Speed condition Straight-line walk period
Temporal synchronization	Latency	If applicable, time the dog took to change speed after the experimenter changed speed. Two values maximum per dog, calculated from GPS data and video recordings.	Experimental group
Gazing behaviour	Gaze towards experimenter	Time in seconds spent with the dog's nose oriented towards the experimenter. Three values per dog, calculated from video recordings.	Experimental group Speed condition Straight-line walk period
	Gaze towards owner	Time in seconds spent with the dog's nose oriented towards the owner. Three values per dog, calculated from video recordings.	Experimental group Speed condition Straight-line walk period
Social attraction to owner	Time before going to owner	If present, length of time in seconds between the beginning of the straight-line walk and the moment when the dog arrived at the owner's feet, which were visible in the Gopro® camera's field.	Experimental group

attractors for their dogs, in our study, the owners were present during the test so that the dogs could go to their owner during the straight-line walk. We therefore recorded whether dogs went to their owner, and if so, how long it took them to do so. We performed a chi-2 test to see if the proportion of dogs who went to their owners differed between the two experimental groups. In the case of the dogs who went to their owners, we performed an ANOVA on the length of time before they went to their owner, with experimental group as a between-subject factor and the dog's sex and age as control predictors.

In all statistical analysis, the normality of distribution and homoscedasticity were graphically checked. Where needed, we performed post-hoc comparisons with the Kenward-Roger approximation and Tukey corrections for multiple testing.

Dogs' behaviours in Phase 1 and temporal synchronization, gazing behaviour and social attraction to the owner in Phase 2 were collected through video recordings. A coder who was unaware of the hypotheses recorded data by visual inspection using Media Player Classic Home Cinema software (version 1.7.13, https://mpc-hc.org/). A second coder who was unaware of the hypotheses independently coded a randomly selected subset of 25% of the data. The inter-rater reliability was assessed by Pearson's correlations. A high level of agreement between raters was found for all the variables (Phase 1: gaze towards the experimenter: $r = 0.98, p < 0.001$; proximity to the owner: $r = 0.99, p < 0.001$; visual attention to an element other than the experimenter: $r = 0.97, p < 0.001$; olfactive attention: $r = 0.94, p < 0.001$; motor inactivity: $r = 0.99, p < 0.001$; Phase 2: latency: $r = 0.99, p < 0.001$; gaze towards the experimenter: $r = 0.98, p < 0.001$; gaze towards the owner: $r = 0.99, p < 0.001$; time before going to the owner: $r = 1.000, p < 0.001$). The coders also examined the experimenter's behaviours to confirm that they behaved consistently with all the dogs during the straight-line walk. We verified that the experimenter followed the speed conditions during the straight-line walk using a LMM: we modelled the experimenter's speed as a function of the speed condition, experimental group and the interaction between these factors as fixed effects. We included dog participants as random effects and an autocorrelation structure of order 1.

3. Results

3.1. Phase 1

3.1.1. Mean distance and mean speed difference between dogs and the experimenter for the two experimental groups

The experimenter's differences in behaviour in the two experimental groups were significant, as a Student t-test confirmed that the mean distance (1.30 ± 0.51 m in the Sync group, 7.22 ± 1.60 m in the Desync group) and the mean absolute difference between the dog's speed and the experimenter's speed (0.24 ± 0.08 m/s in the Sync group, 0.84 ± 0.14 m/s in the Desync group) were smaller for dogs in the Sync group compared to dogs in the Desync group (mean distance: $t_{18} = 14.05$, $P < 0.001$, Cohen's $d = 4.97$; mean absolute difference between the dog's speed and the experimenter's speed: $t_{24} = 14.63$, $P < 0.001$, Cohen's $d = 5.17$).

3.1.2. Dog behaviours

For a period of 15 minutes, the experimenter synchronized or desynchronized their locomotion to that of the dog. Our ANOVA full results are reported in Table 2 in the Supplemental File 1. There was a significant effect of experimental group on the dogs' gaze towards the experimenter ($F_{1,28} = 23.56$, $P < 0.001$, Cohen's $d = 1.97$) and on the proximity to the owner ($F_{1,28} = 11.72$, $P = 0.002$, Cohen's $d = 0.97$). Dogs in the Sync group spent less time gazing at the experimenter and spent less time close to their owner compared to dogs in the Desync group (Fig. 2). There was no significant difference between the two experimental groups regarding visual attention to an element other than the experimenter, olfactive attention or motor inactivity (see Table 2 in the Supplemental File 1). We established a rule to keep the dog's attention focused on the experimenter: if the dog did not look at the experimenter for 1 minute, the experimenter called the dog's name. Since all the dogs looked in the direction of the experimenter at least once per minute, this rule was ultimately unnecessary. Additionally, another rule was established to prevent the dogs from remaining inactive for extended periods: the experimenter called the dogs by their name after one minute of inactivity. This occurred for 17 dogs (8 from the sync group, 9 from the desync group). Among these 17 dogs, 9 continued to remain inactive (2 from the sync group, 7 from the desync group), prompting their owners to call them after 2 minutes of inactivity. For 2 dogs (1 from the sync group and 1 from the desync group), the owner's call was insufficient, and after 3 minutes of inactivity, the owner took a few steps and it re-engaged the dog in activity.

3.2. Phase 2

3.2.1. Experimenter's compliance to the experimental protocol

Naive coders' visual inspection confirmed that during the straight-line walk, the experimenter behaved consistently with all dogs: they maintained a neutral facial expression, remained silent, looked at their phone and never turned their head throughout the entire walk. The analysis of the experimenter's speed data obtained from GPS data further confirmed that the experimenter complied with the speed conditions ($\chi_2 = 619.35$, 2, $P < 0.001$; post-hoc tests: fast walk-slow walk: estimate ± SE = 0.37 ± 0.05, $t_{60} = 8.39$, $P < 0.001$, Cohen's $d = 1.24$; fast walk-static: estimate ± SE = 1.10 ± 0.05, $t_{60} = 24.49$, $P < 0.001$, Cohen's $d = 3.63$; slow walk-static: estimate ± SE = 0.72 ± 0.05, $t_{60} = 16.09$, $P < 0.001$, Cohen's $d = 2.39$), with no differences between the two experimental groups ($\chi_1 = 0.79$, $P = 0.374$).

3.2.2. Location synchronization

For the straight-line walk, we measured the distance between the dog and the experimenter and the time spent near the experimenter. The full LMM results are reported in Table 3 in the Supplemental File 1. There was an effect of experimental group on the two variables (LMM of the distance between the dog and the experimenter: $\chi^2_1 = 10.15$, $P < 0.001$, Cohen's $d = 0.77$; LMM of the time spent near the experimenter: $\chi^2_1 = 9.90$, $P < 0.001$, Cohen's $d = 0.68$). The dogs in the Sync group stayed closer to the experimenter (Fig. 3.A) and spent more time near the experimenter (Fig. 3.B) compared to dogs in the Desync group. There was also an effect of straight-line walk period on these two variables (LMM of the distance between the dog and the experimenter: $\chi 2_2 = 37.51$, $P < 0.001$; post-hoc tests: first period – second period: estimate ± SE = —7.26 ± 2.03, $t_{48} = —3.58$, $P = 0.002$, Cohen's $d = —0;94$; first period – third period: estimate ± SE = —12.45 ± 2.06, $t_{48} = —6.05$, $P < 0.001$, Cohen's $d = —1.62$; second period – third period: estimate ± SE = —5.19 ± 2.15, $t_{48} = —2.42$, $P = 0.050$, Cohen's $d = —0.68$; LMM of the time spent near the experimenter: $\chi 2_2 = 80.31$, $P < 0.001$; post-hoc tests: first period – second period: estimate ± SE = 5.77 ± 0.97, $t_{48} = 5.95$, $P < 0.001$, Cohen's $d = 4.30$; first period – third period: estimate ± SE = 8.51 ± 0.98, $t_{48} = 8.66$, $P < 0.001$, Cohen's $d = 6.30$; second period – third period: estimate ± SE = 2.74 ± 1.02, $t_{48} = 2.67$, $P = 0.027$, Cohen's $d = 2.04$). For all the dogs, the distance between the dog and the experimenter increased over the course of the test (Fig. 3.A) and the time spent near the experimenter decreased over the course of the test (Fig. 3.B). There was no effect of speed condition on these two variables (see Table 3 in the Supplemental File 1).

3.2.3. Activity synchronization

To study activity synchronization, we calculated the dog's speed and the experimenter's speed, then we analyzed the speed difference and the time spent at a similar speed. The full LMM results are reported in Table 4 in the Supplemental File 1.

Regarding speed difference, we found a significant interaction between experimental group and speed condition (LMM: $\chi 2_2 = 11.29$, $P =$

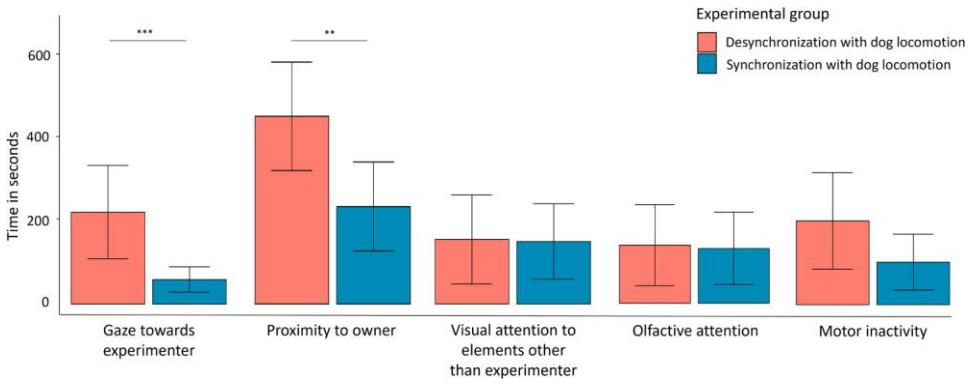


Fig. 2. Dog behaviours for each experimental group during Phase 1. Data are presented as mean ± *SD*. *** $P \leq 0.001$, ** $0.001 < P \leq 0.01$.

0.004), and a significant interaction between experimental group and straight-line walk period (LMM: $\chi 2_2 = 12.81$, $P = 0.002$). Post-hoc tests (see Table 5 in the Supplemental File 1) showed that dogs in the Desync group had a higher speed difference in the fast-walk condition than in all the other conditions (Fig. 4.A). They also had a higher speed difference than dogs in the Sync group during the first period of the test (Fig. 4.B).

Regarding the time the dog spent at a similar speed to the experimenter, there was a significant interaction between experimental group and speed condition (LMM: $\chi 2_2 = 17.33$, $P < 0.001$) and a significant interaction between experimental group and straight-line walk period (LMM: $\chi 2_2 = 11.29$, $P = 0.004$).

Post-hoc tests (see Table 5 in the Supplemental File 1) showed that in both experimental groups, dogs spent less time at a speed similar to that of the experimenter in the fast-walk condition compared to the static condition (Fig. 5.A). Dogs in the Desync group spent less time at a speed similar to that of the experimenter in the slow-walk condition compared to the static condition (Fig. 5.A). Dogs in the Sync group spent more time at a speed similar to that of the experimenter during the first straight-line walk period compared to the third straight-line walk period (Fig. 5.B).

3.2.4. *Temporal synchronization*

The experimenter changed their speed twice during the straight-line walk. Eleven out of 32 dogs adjusted their speed accordingly. The proportion of dogs who adjusted their speed did not differ by experimental group ($\chi 2_1 = 0.55$, $P = 0.772$). For dogs who exhibited latencies, they adjusted their speed in 1.62 s ± 1.28 s, with no effect of experimental group (see full LMM results in Table 6 in the Supplemental File 1).

3.2.5. *Gazing behaviour*

We measured dogs' gaze towards the experimenter and towards the owner during the straight-line walk. Dogs spent 4.63 s ± 3.68 s per straight-line walk period gazing at the experimenter and 3.85 s ± 3.78 s per straight-line walk period gazing at their owner, with no effect of experimental group, straight-line walk period or speed condition on these variables (see full LMM results in Table 7 in the Supplemental File 1).

3.2.6. *Social attraction*

Fourteen dogs went to their owners before the end of the straight-line walk. The proportion of dogs who went to their owners did not differ by experimental group ($\chi 2_1 = 1.14$, $P = 0.143$). In the case of the dogs who went to their owners, we analyzed the time it took them to do so (see ANOVA results are reported in Table 8 in the Supplemental File 1). We found a significant effect of experimental group on the length of time before going to the owner ($F_{1,10} = 7.42$, $P = 0.021$, Cohen's $d = 1.86$), as dogs in the Desync group went to their owner more quickly than dogs in the Sync group (Fig. 6).

4. Discussion

To explore the consequences of dogs' direct sensitivity to human behaviours on dogs' behavioural synchronization, we conducted an experiment in which an unfamiliar person synchronized or desynchronized their locomotion with that of the dogs. We hypothesized that dogs with whom they had previously synchronized their locomotion would then exhibit stronger behavioural synchronization with them compared to dogs with whom they had not synchronized their locomotion. Our hypothesis was validated for two components of behavioural synchronization, namely location and activity synchronization, but not for temporal synchronization. Our results extend those of a previous study (Duranton et al., 2019b): the authors found that dogs had a social preference for an unfamiliar person who had synchronized with them. Human synchronization with dogs affects dogs' social preference, a specific choice, and we have demonstrated that it influences their behavioural response, as the dogs' perception of the experimenter's motor behaviour affected the dogs' motor response.

The experimenter either synchronized or not with the dog for 15 minutes. We observed behavioural differences between the two experimental groups during this phase. Indeed, dogs in the desynchronization with dog locomotion (Desync) group spent more time looking at the experimenter and spent more time at their owner's feet than dogs in the synchronization with dog locomotion (Sync) group. Since the owners were inactive and considering that dogs tend to synchronize with their owner, a rule was implemented to prevent the dogs from being inactive for too long. It is true that this rule may have influenced the dogs' behaviour because calling the dogs by their name attracts their attention. However, the number of dogs called by the experimenter was equivalent between the two experimental groups, so the difference in visual attention towards the experimenter was not due to the experimenter's calls. A more parsimonious explanation is that synchronizing with the dogs is a known behaviour, since dogs are accustomed to synchronizing with their owners during walks (Foltin, 2021; Gaunet et al., 2014), while desynchronizing with the dogs is an unusual behaviour. Faced with this unusual situation, dogs thus engaged in social referencing (Duranton et al., 2016; Merola et al., 2012): they looked at the unfamiliar person and their owner (hence the greater visual attention to the experimenter in the Desync group) and synchronize with their owner (hence the greater time spent close to their owner in the Desync group). One might think that the increased time spent close to their owner was because more dogs in the Desync group were called by their owner, but the dogs did not necessarily go to their owner after these calls. We propose that dogs that spent more time near their owner were seeking information from them through social referencing. However, this seeking of information from the owner could also have been accompanied by a search for security in this unfamiliar situation. It is thus possible that dogs in the Desync group gazed longer at the unfamiliar person not only to seek information but also because the person's

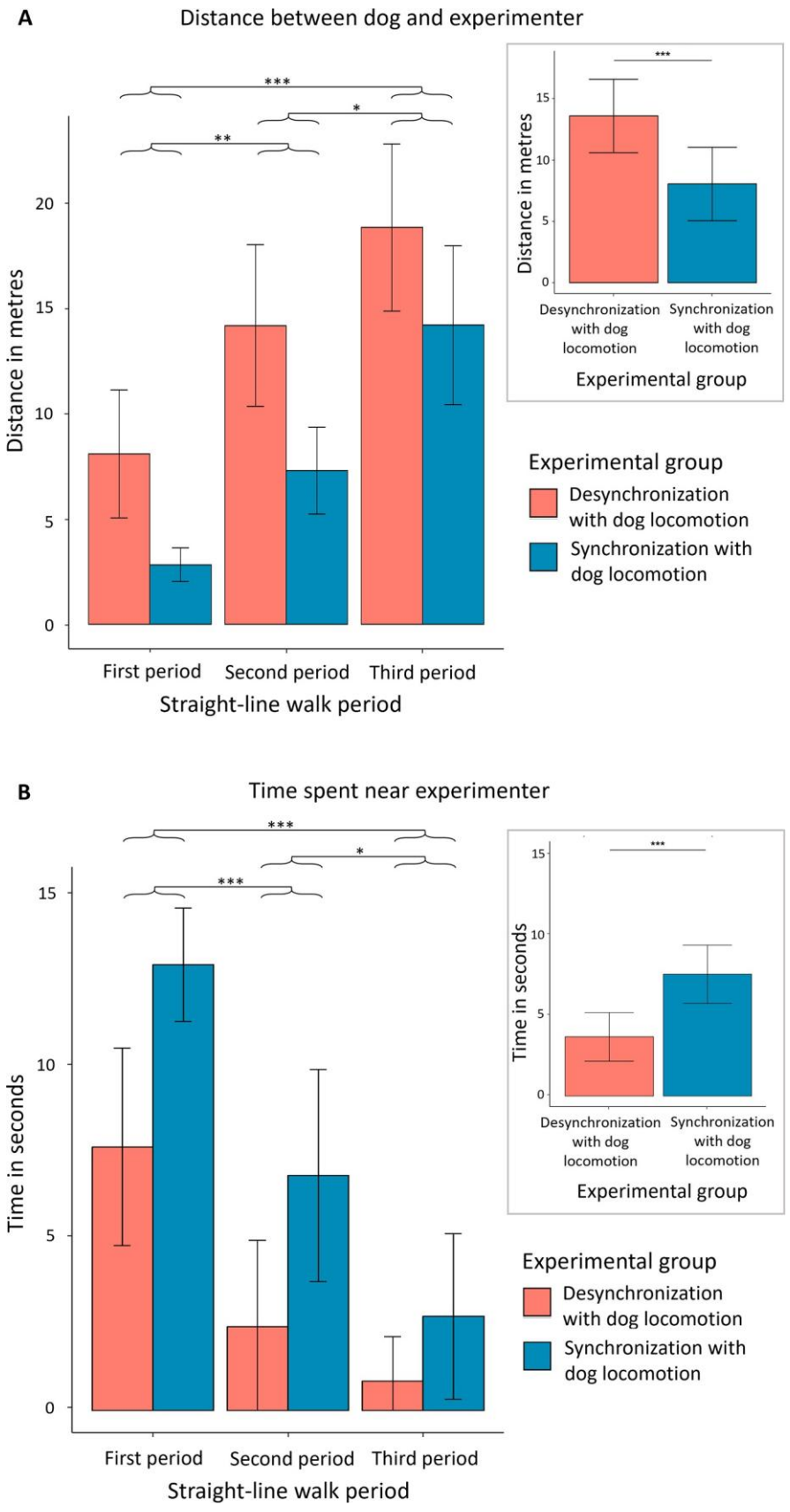


Fig. 3. Effect of experimental group and straight-line walk period on the distance between the dog and the experimenter (A) and on the time spent by the dog near the experimenter (B). Data are presented as mean ± *SD*. * $0.01 < P \leq 0.05$, ** $0.001 < P \leq 0.01$, *** $P \leq 0.001$.

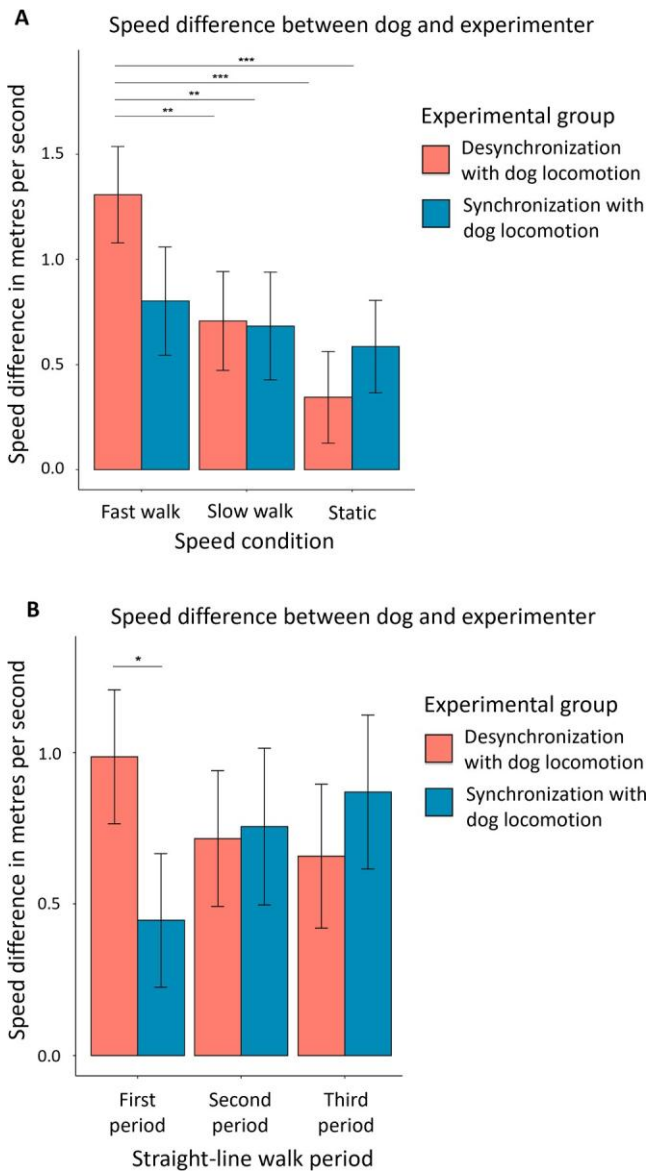


Fig. 4. Significant interaction between experimental group and speed condition on the speed difference (A) and significant interaction between experimental group and straight-line walk period on the speed difference (B). Data are presented as mean ± *SD*. * $0.01 < P \leq 0.05$, ** $0.001 < P \leq 0.01$, *** $P \leq 0.001$.

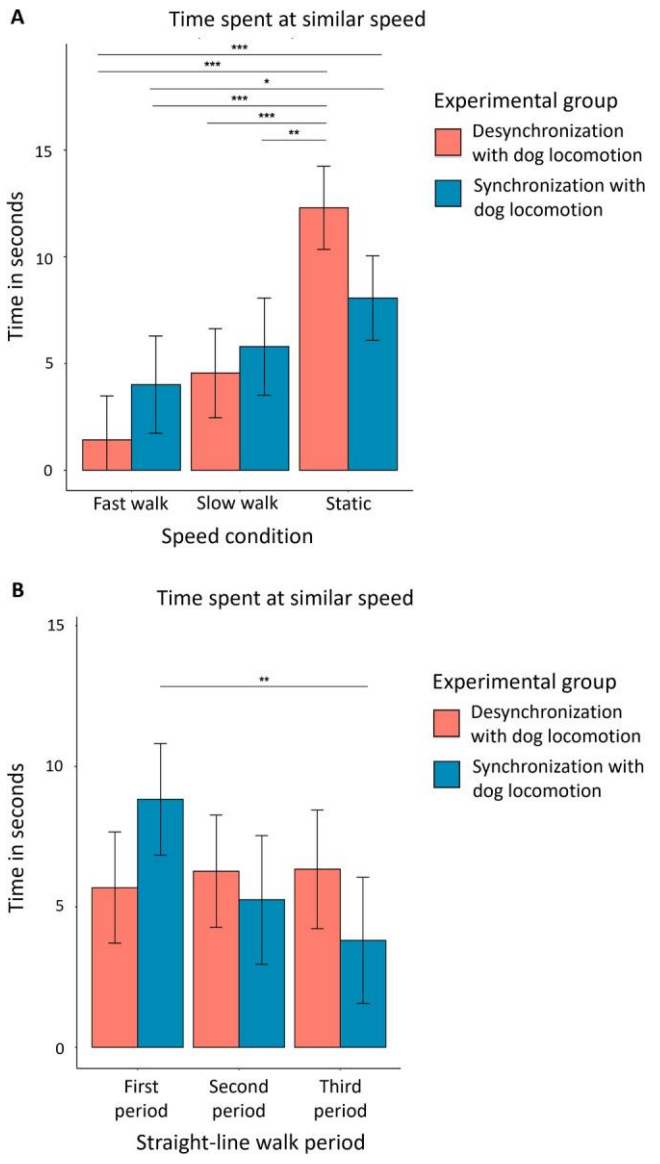


Fig. 5. Significant interaction between experimental group and speed condition on the time spent at a similar speed (A) and significant interaction between experimental group and straight-line walk period on the time spent at a similar speed (B). Data are presented as mean ± *SD*. * $0.01 < P \leq 0.05$, ** $0.001 < P \leq 0.01$, *** $P \leq 0.001$.

unusual behaviour induced insecurity in these dogs. Therefore, dogs' gaze activity could be associated with both information-seeking and monitoring of the person's behaviour. Ultimately, gaze behaviour may reflect the dog's cognitive and emotional state towards the unfamiliar person. Although we did not detect behavioural signals of appeasement or discomfort in these dogs, we cannot rule out the possibility that they were in a more uncomfortable physiological state compared to the other dogs. Future studies should therefore consider collecting physiological data, such as heart rate or respiratory rate, to determine the dogs' physiological arousal in addition to their behavioural response.

Synchronizing with the dogs has thus a direct consequence on their behaviour: dogs engage in less social referencing and behave as they would during a walk with a familiar person. This is reflected in the straight-line walking task, where they synchronize more with the experimenter. Indeed, during the straight-line walk, dogs in the Sync group stayed closer and spent more time in proximity to the experimenter compared to dogs in the Desync group (location synchronization). In addition, at the beginning of the straight-line walk, the dogs' speed in the Sync group was closer to the experimenter's than dogs in the Desync group (activity synchronization). Dogs in the Sync group adjusted their speed better at the beginning of the test, but the difference between the two experimental groups faded during the test. Finally, there was no difference between the two experimental groups regarding dogs' speed adjustment to the experimenter's change in speed (temporal synchronization). Previous studies using similar protocols focused on pet dogs' locomotor synchronization with their owner and showed that dogs exhibit location, activity and temporal synchronization during walks with their owner (Duranton et al., 2018, Lamontagne et al., 2023). Regarding temporal synchronization, dogs adjust their own speed within 2 seconds when owners change their walking rhythm. Considering the reaction time for dogs to perceive the change and adjust their movement accordingly, we can deduce that dogs adapt their locomotion almost instantly in response to changes in their owner's walking rhythm, indicating a high degree of sensitivity and responsiveness to their owner's movements. Our findings suggest that this sensitivity depends on affiliation, because only one-third of the dogs in our study adjusted

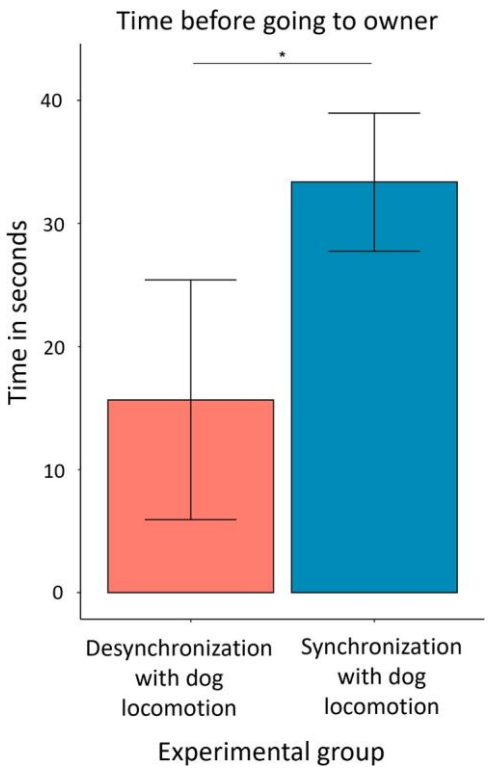


Fig. 6. Effect of experimental group (desynchronization with dog locomotion: $n = 9$, synchronization with dog locomotion: $n = 5$) on the time before going to the owner during the straight-line walk. Data are presented as mean ± *SD*. ** $0.001 < P \leq 0.01$.

their speed following the experimenter's change of speed. This suggests that dogs' temporal synchronization with an unfamiliar person is less pronounced than that observed with their owner. Furthermore, we found no significant difference between the two experimental groups regarding this component of behavioural synchronization. This indicates that the behaviour of an unfamiliar person affects the dogs' locomotor behaviour in a broad way, impacting their proximity to the person and their overall speed, but this influence does not extend to finer behavioural adjustments, such as making precise changes in speed immediately following the person's change of walking rhythm.

It is worth noting that over the course of the straight-line walk, the dogs in both experimental groups gradually moved away from the experimenter. This is explained by the fact that dogs have a tendency of going to their owner, as demonstrated in previous studies showing the social attractor effect of owners for dogs (Duranton et al., 2017b, 2018; Kerepesi et al., 2015; Lamontagne et al., 2023). Dogs follow their owner more than either a familiar or an unfamiliar person when all three simultaneously walk away from the dog (Kerepesi et al., 2015). Also, dogs systematically move away from and then return to their owner during walks, as if an invisible rubber band were connecting them to their owner (Foltin, 2021; Lamontagne et al., 2023). Our study confirmed this social attraction, and also highlighted a new insight: social attraction to the owner was delayed when the unfamiliar person had synchronized their locomotion with the dog's. This was demonstrated by the fact that the dogs in the Sync group went to their owners later than the dogs in the Desync group. In other words, synchronizing with dogs temporarily redirects the social attraction effect of the owner. However, given the limited number of dogs that went to their owner during the straight-line walk (9/16 in the Desync group and 5/16 in the Sync group), other studies involving a larger sample of dogs are necessary to confirm this result.

Dogs usually tend to synchronize with familiar people. It is therefore possible that the unfamiliar person' synchronization upon the dogs leads to the dogs perceiving that person as familiar, thereby explaining the subsequent dogs' synchronization with that person. The dogs' direct sensitivity to unfamiliar human's behaviour evidenced in our study could stem from a learned and reinforced process acquired by dogs over their lifetime as they live with humans on a daily basis (Feuerbacher and Wynne, 2012; Soproni et al., 2001; Udell et al., 2010). The tendency of dogs to synchronize with familiar people could indeed result from associative learning, as it is often rewarding for dogs due to the time spent and the quality of interactions with these people. Moreover, dogs may experience feelings of security and positive emotions when synchronizing with familiar people, reinforcing the association between synchronization and positive outcomes, thereby enhancing dogs' inclination to synchronize with familiar people. Some authors posit that domestication has led to dogs' ability to read human behaviours and adapt their behaviour accordingly (Lazzaroni et al., 2020; Miklósi et al., 2003, 2004; Riedel et al., 2008; Savalli et al. (2016); Vas et al., 2005, 2008). This argument is supported by the fact that wolves, even when reared by humans, adjust their behaviour less with that of humans compared to dogs (Gácsi et al., 2013; Hare et al., 2002; Lazzaroni et al., 2020), and that dogs demonstrate more approaching behaviours and gaze towards unfamiliar persons compared to wolves (Bentosela et al., 2016).

A cognitive mechanism that could also be at play during the straight-line walk is motor contagion. It occurs when the perception of a behaviour leads to its execution by the observer, leading to behavioural synchronization (Cracco and Brass, 2018; Roberts et al., 2016). It is possible that dogs' perception of the unfamiliar person's locomotor behaviour led to the dogs' locomotor synchronization with the person. In primates, motor contagion relies on motor resonance through the activation of mirror neurons (Brass and Heyes, 2005; Rizzolatti et al., 2001; Rizzolatti and Craighero, 2004; Uithol et al., 2011). These motor neurons are activated when a subject executes a behaviour or perceives the execution of that behaviour by a third party (Rizzolatti et al., 2001; Rizzolatti and Craighero, 2004). When one individual perceives another performing a behaviour, motor resonance occurs if the representations related to the behaviour are simultaneously activated in both individuals, making the observer more likely to execute the behaviour (Bidet-Ildei et al., 2011; Rizzolatti et al., 2009; Uithol et al., 2011). When two humans walk side by side, motor resonance occurs and the activation of mirror neurons in both individuals is responsible for the spontaneous synchronization of their gait. While no studies have investigated the existence of mirror neurons in dogs, these neurons may be an elementary brain system resulting from evolutionary conservation present in all social mammals (Bonini et al., 2022; Pörtl and Jung, 2017). Our results indicate the occurrence of motor contagion at the interspecific level, and pave the way for further studies to investigate whether interspecific behavioural synchronization relies on the activation of canine and human mirror neurons.

For the first time, we have identified the specific behaviour an unfamiliar person should exhibit in the presence of the owner to promote behavioural synchronization of the dog with that person. Our findings have direct implications for people who interact with dogs on a daily basis. Understanding dogs' behavioural responses during encounters with unfamiliar people is a key factor for people who interact with dogs in everyday life (Kerepesi et al., 2015), most notably the fact that a dog's locomotor response depends on the locomotion of the unfamiliar person. Research shows that when a person exhibits friendly behaviour, pets a dog with long, smooth strokes and scratching their body and ears, or speaks softly to a dog for 15 minutes, dogs show elevated serum levels of endorphin, oxytocin, prolactin, and dopamine, neurotransmitter hormones related to reward and social bonding circuits (Odendaal and Meintjes, 2003). However, it is not always possible to establish physical contact with the dog. For instance, if a dog has run away and is roaming the streets, it can be dangerous for an unfamiliar person to attempt to touch the dog for capture. Our study shows that unfamiliar people may not necessarily need to make immediate physical contact with dogs

during initial interactions: following dogs and adjusting one's speed to a dog's increases dogs' behavioural synchronization. In the case of a runaway dog, if a person takes the time to synchronize with the dog without touching or directly staring at the dog, there is a higher likelihood that the dog will align with the person in return, making the capture easier and reducing stress for the dog. Similarly, in dog boarding facilities, dogs are often walked by unfamiliar individuals. If these individuals synchronize themselves with the dog, it reduces the risk of the dog straying too far during walks. It is worth noting that in our protocol, dogs were off-leash allowing them complete freedom of movement. However, in daily life, dogs are often walked on-leash. This raises the question of whether our findings are applicable to on-leash walks. Despite the restricted movement when on-leash, behavioural synchronization between dogs and humans still occurs (Gaunet et al., 2014). Our findings could thus potentially extend to on-leash walks: adjusting to a dog's locomotion could result in the dog being closer to the person and better adjusting their pace to that of the person during on-leash walks. Consequently, our results could aid in facilitating dogs' adjustment to unfamiliar people during walks. Nonetheless, it is important to note that dogs' behaviour during on-leash walks is highly influenced by learning: many dogs have learned to walk at heel when on-leash. This learning involves staying close to the human and adopting the same pace, which essentially amounts to synchronizing with the human. It is therefore likely that dogs trained to walk at heel when on-leash would synchronize with the unfamiliar person as soon as they are leashed, even if the person has not previously adjusted to them. As a final point, this method of behavioural synchronization could also be used for dogs uncomfortable with unfamiliar people to modify their behaviour towards these people. Unfamiliar human synchronizing with the dogs can indeed create positive experiences for the dogs, gradually associating unfamiliar people with positive interactions and reducing their stress. We suggest the use of human behavioural synchronization to facilitate interactions between anxious dogs and unfamiliar people, but its effectiveness in this context needs further research, as our study involved only non-anxious dogs comfortable with unfamiliar people. Finally, our study provides a new tool to help manage interactions between dogs and unfamiliar people in a variety of situations in daily life in which the owner is present.

Besides these implications, like all studies, the current study has limitations. First, we conducted the tests in an open and natural environment to ensure there were no spatial constraints for the dogs. However, this outdoor space could have contained various odors, including those of previously tested dogs, and probably those of other animals, such as birds, cats and rabbits. We assume that the scents of previously tested dogs were overshadowed by the multitude of other odors present, thus having minimal influence on the behaviour of subsequent dogs. However, the overall array of scents in the environment may have impacted the behaviour of the dogs in general. It is possible that the dogs would have reacted differently, especially in terms of their olfactory attention, if the study had been conducted in an empty room. Also, the dogs were off-leash in this open area, which necessitated the recruitment of dogs with good recall in case they strayed from the test area. Another recruitment bias was that we selected dogs comfortable with unfamiliar people for the study to avoid inducing stress in the participating dogs. We acknowledge that these selection criteria make our sample less representative of the overall domestic canine population. Additionally, since recruitment was based on voluntary participation, through posters in dog parks and on social media, the owners who participated were inherently interested in their dog's behaviour and more broadly in dog-human interaction. This type of dog-owner relationship may have an influence on the dogs' behaviour and their reaction to an unfamiliar person. Moreover, the presence of the owner in our study likely impacted the dogs' behaviour. Previous studies have demonstrated that dogs behave differently when their owner is absent, often displaying more passive behaviour and waiting towards the exit where their owner left (Mariti et al., 2018; Palestrini et al., 2005; Prato-Previde et al., 2003; Topál et al., 1998). Having the owner present was necessary in our study location, as there was a high likelihood that the dogs would have left the test area to go to their owner otherwise. Finally, we positioned all owners at the same position to not have variation in the owner's location. However, we did not anticipate that nearly half of the dogs would go to their owner before the end of the straight-line walk. It would have been interesting to vary the owner's position, either to one side or the other with respect to the straight-line walking zone, to carefully verify that the dogs were indeed attracted to the owner and not just to the same side of the field.

5. Conclusion

We explored the effect of an unfamiliar person's behavioural synchronization upon dogs on the dogs' subsequent behavioural response towards the person, in an open outdoor environment. Our study demonstrated that maintaining a silent proximity of 1 m from the dogs and aligning with their speed, i.e. with an average speed difference of 0.2 m/s, significantly enhanced the dogs' behavioural synchronization with the unfamiliar person. Given that dogs usually synchronize with familiar people, these findings show that synchronizing with dogs is a way of becoming familiar with them; and it leads to motor contagion at the interspecific level, as dogs subsequently synchronized their locomotion with the person starting walking. Our study contributes to the comprehension of the properties of interspecific behavioural synchronization, and also bears practical implications. We indeed provide a novel, easily implementable tool for familiarizing with dogs, particularly useful in situations where direct contact or offering food is impractical. Our approach thus offers a valuable method for effectively managing interactions between dogs and unfamiliar people in everyday life.

Authors' contributions

All authors contributed to the study conception and design. Material preparation and data collection and processing were carried out by Angélique Lamontagne and Thierry Legou. Statistical analyses were carried out by Angélique Lamontagne. The first draft of the manuscript was written by Angélique Lamontagne, and all authors commented on previous versions of the manuscript. All authors gave final approval for publication and agreed to be held accountable for the work.

Funding

This work was supported by the National Association for Research and Technology (ANRT), the association *Agir pour la Vie Animale*, the French National Centre for Scientific Research (CNRS), and Aix-Marseille University.

CRediT authorship contribution statement

Angélique Lamontagne: Writing – original draft, Methodology, Formal analysis, Data curation, Conceptualization. **Thierry Legou:** Writing – review & editing, Methodology, Data curation, Conceptualization. **Thierry Bedossa:** Writing – review & editing, Funding acquisition, Conceptualization. **Florence Gaunet:** Writing – review & editing, Supervision, Methodology, Funding acquisition, Conceptualization.

Declaration of Competing Interest

The authors declare that they have no known competing financial

interests or personal relationships that could have appeared to influence the work reported in this paper.

Data availability

Datasets are accessible in the Open Science Framework repository at the following link: http://osf.io/bq648/?view_only= f1de205998c84862a427371c2949adb3.

Acknowledgements

The authors are grateful to the owners who volunteered for the study. The authors also thank Camille Valle and Gael Montredon for the coding of the video recordings.

Appendix A. Supporting information

Supplementary data associated with this article can be found in the online version at doi:10.1016/j.applanim.2024.106204.

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2.2. La synchronisation de la marche d'une personne inconnue sur celle du propriétaire augmente ultérieurement la synchronisation du chien sur la personne

Nous avons poursuivi l'exploration de l'effet du comportement d'une personne inconnue sur la synchronisation locomotrice des chiens envers cette personne, cette fois en impliquant activement les propriétaires. Le lien qui unit les chiens et leurs propriétaires est particulier : les propriétaires sont les partenaires d'interaction privilégiés des chiens (Carlone et al., 2019), leur référence sociale (Merola et al., 2012a) et exercent une forte attraction sociale (Lamontagne et al., 2024a, 2024b). Nous avons investigué la réponse comportementale des chiens lorsque la synchronisation locomotrice d'une personne inconnue est dirigée non pas vers eux, mais vers leurs propriétaires. Considérant la sensibilité des chiens envers le comportement de leurs propriétaires, nous avons émis l'hypothèse que la synchronisation locomotrice entre une personne non familière et le propriétaire induirait la synchronisation locomotrice du chien sur la personne ensuite.

Nous avons repris le protocole de l'étude présentée dans la section précédente, pour permettre une comparaison directe entre les deux études. Pour les chiens du premier groupe expérimental, j'ai synchronisé ma locomotion sur celle du propriétaire, tout en discutant avec ce dernier, pendant 15 minutes. Pour les chiens du second groupe expérimental, je n'ai pas interagi avec le propriétaire et j'ai désynchronisé ma locomotion par rapport à la sienne pendant la même durée. Comme dans l'étude précédente, j'ai ensuite comparé la synchronisation locomotrice des chiens des deux groupes expérimentaux pendant que je marchais en ligne droite. Pendant cette marche, les propriétaires étaient neutres et statiques, au même emplacement que celui utilisé dans l'étude précédente.

Les résultats obtenus sont proches de ceux de l'étude précédente, c'est-à-dire une plus forte synchronisation locomotrice des chiens du premier groupe expérimental par rapport au second groupe, et ce de manière temporaire, les chiens ayant tendance à revenir vers leur propriétaire avant la fin de la marche en ligne droite.

Nous avons ainsi montré que les chiens sont sensibles aux interactions entre leur propriétaire et une personne inconnue et que se synchroniser avec les chiens ou avec les propriétaires engendre une réponse comportementale similaire de la part des chiens. Ces deux études apportent des informations précieuses sur les comportements que nous pouvons adopter au quotidien envers les chiens non familiers ou leurs propriétaires, donnant ainsi des clés pour optimiser la gestion des rencontres entre les chiens et les nouvelles personnes dans la vie de tous les jours.

Article 3 : Lamontagne, A., Legou, T., Bedossa, T., & Gaunet, F. (2024). Walk with me? Part 2: Dogs synchronize with an unfamiliar person who first synchronized with their owner. *Applied Animal Behaviour Science, 275*, 106271

https://doi.org/10.1016/j.applanim.2024.106271

Applied Animal Behaviour Science 275 (2024) 106271



Contents lists available at ScienceDirect

Applied Animal Behaviour Science

journal homepage: www.elsevier.com/locate/applanim



Walk with me? Part 2: Dogs synchronize with an unfamiliar person who first synchronized with their owner

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ARTICLE INFO

Keywords:
Behaviour
Canine
Interspecific synchronization
Motor contagion
Social referencing
Indirect sensitivity

ABSTRACT

Dogs exhibit sensitivity to human behaviours directed towards them (see Part 1), but dogs' sensitivity to human third-party interactions, i.e. eavesdropping or indirect sensitivity, remains unclear. This study aimed to investigate dogs' indirect sensitivity in an ecological context devoid of food incentives. We thus explored dogs' responsiveness to interactions between their owner and an unfamiliar person during a synchronous walk in an outdoor environment. To do so, we delineated two experimental groups of pet dogs: an unfamiliar experimenter either walked and talked with the owner for 15 minutes, maintaining a 1-metre proximity and aligning speed (n = 16 dogs) or stayed away from the owner for 15 minutes (n = 16 dogs) in the dog's presence. We then compared the dogs' locomotor synchronization with the experimenter and the dogs' gaze behaviour during a straight-line walk. Dogs for which the experimenter had interacted with the owner displayed enhanced location, temporal and activity synchronization with the experimenter during the straight-line walk compared to dogs for which the experimenter had not interacted with the owner. Specifically, these dogs were closer to the experimenter, had a smaller speed difference compared to the experimenter's speed at the beginning of the straight-line walk, and more dogs from this group adjusted their speed directly after the experimenter's change of speed. Regarding dogs' gaze behaviour, we did not find significant differences between the two experimental groups. Finally, we found that dogs from both experimental groups were attracted to their owner during the straight-line walk. Our results demonstrate, for the first time, that dogs' behavioural synchronization with an unfamiliar person occurs subsequently to the dogs' perception of intraspecific behavioural synchronization between their owner and the unfamiliar person. This third-party sensitivity may result from an automatic process of reproducing perceived behaviours, suggesting interspecific motor contagion when dogs perceive synchronous behaviour of two human agents; and/or from a transitivity of familiarity, the unfamiliar person becoming indirectly familiar to the dogs through their interaction with the dogs' owners. These findings bear practical significance, as encounters between unfamiliar people and dog-owner dyads can be enhanced if those people first synchronize and talk with dogs' owners before interacting with dogs.

1. Introduction

Dogs are sensitive to human social cues, and direct human behaviours affect dog behaviours (Lamontagne et al., 2024). Whether dogs are sensitive to human third-party interactions, also called indirect sensitivity or eavesdropping (Bonnie and Earley, 2007), however, has been subject to debate. Eavesdropping develops very early on in human infants (Callaghan et al., 2022; Hamlin et al., 2007; Matheson et al., 2013; Nielsen et al., 2012; Repacholi and Meltzoff, 2007; Repacholi et al., 2014) and has also been studied in the chimpanzee (Herrmann et al., 2013; Subiaul et al., 2008). It allows an individual to use information from others' behaviour without the costs of direct experience. Eavesdropping may thus serve to learn by observing the behaviour of others, even without direct involvement in the interaction (Abdai and Miklo´si, 2016). However, eavesdropping necessitates cognitive engagement, as observers must attend closely to the interacting parties to avoid missing contextual cues, and they must accurately recall the relationship dynamics between the two individuals (rather than solely focusing on one

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https://doi.org/10.1016/j.applanim.2024.106271
Received 2 January 2024; Received in revised form 29 April 2024; Accepted 30 April 2024
Available online 5 May 2024
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individual), as the nature of observed interactions may vary depending on the social context (Subiaul et al., 2008).

Studies conducted with dogs have not yielded unanimous results. At the intraspecific level, some authors (Cools et al., 2008; Ward et al., 2009) have found that dogs jump on, bite at, or mount the losing individual when the dogs observe a playful interaction between two conspecifics. Dogs thus use indirect signals obtained by observing interactions between conspecifics to behave accordingly. Another study shows that dogs prefer to first approach the winner rather than the loser in a game of tug-of-war between dogs or between a dog and a human (Rooney and Bradshaw, 2006). This result suggests that dogs can derive information regarding the outcome of intraspecific and interspecific interactions, influencing their behaviour, as indicated by their preference for approaching individuals perceived as successful in non-agonistic interactions. Other studies have examined whether dogs eavesdrop when they are spectators of interactions between humans (Freidin et al., 2013; Kundey et al., 2011; Marshall-Pescini et al., 2011). In these studies, dogs observed interactions between two people carrying food and a third person requesting food. The dogs then chose the person who gave the food to the third person more often than the person who did not. If the dogs observed the two people carrying the food without the third person present, they chose randomly, suggesting that they made their choice based on information obtained from observing the interaction (Marshall-Pescini et al., 2011). Finally, if the people carrying food acted neutrally, but the third person accepted food from one and refused food from the other, then the dogs preferentially approached the person whose food was accepted by the third person (Freidin et al., 2013).

However, other studies using similar experimental paradigms have obtained different results. In these studies, dogs paid attention to interactions between two people or between a person and a dog (Nitzschner et al., 2012, 2014; Yong and Ruffman, 2015), but they did not use indirect information: when choosing between two boxes of food, dogs did not preferentially choose the box that one person indicated verbally or pointed out (Kaminski et al., 2012). Similarly, when choosing between two people, one who helped a third to open a box of food and the other who did not (Jim et al., 2020), or one who fed a demonstrator dog and the other who did not (Jim et al., 2022), dogs did not preferentially choose the person who helped or fed the third party. It is worth noting that in these studies, the dogs could not see the food as it was in a box. It is possible that due to this lack of visibility, cues provided by the humans may not have been perceived as directly linked to obtaining food. In contrast, in studies where dogs demonstrated eavesdropping behaviour, the food was visible to the dogs, potentially fostering a direct association between the observed third-party interaction and the prospect of obtaining food. Taken together, these mixed results indicate that dogs appear to be sensitive only to certain types of third-party interactions, when the outcome of the interaction is clear, visible or attractive to the dogs. Another possibility is that their lack of indirect sensitivity in certain situations is due to the identity of the interacting agent. In another study involving the dogs' owners (Chijiiwa et al., 2015), dogs approached a neutral person more frequently than a person who had refused to assist their owner in opening a jar. The dogs' eavesdropping ability in this study may have been due to the owner's involvement in the interaction. Dogs are indeed particularly attentive to their owner's social cues (Gaunet, 2008, 2010; Gaunet and Deputte, 2011; Marshall-Pescini et al., 2009; Miklo´si et al., 2000; Prato-Previde et al., 2007; Szetei et al., 2003; Vir´anyi et al., 2006) and in new situations, such as a new object (Merola et al., 2012a, 2012b, 2014) or a unfamiliar person (Duranton et al., 2016; Salamon et al., 2020), dogs exhibit social referencing: they seek information from their owner and adjust their behavioural response based on their owner's behaviours. Interestingly, dogs exhibit social referencing with their owner but not with an unfamiliar person, suggesting that although dogs are sensitive to human social cues, their responses towards a new stimulus depend on their familiarity with the human (Merola et al., 2012a; Duranton and Gaunet, 2016; Duranton et al., 2017a).

In Part 1 (Lamontagne et al., 2024), we demonstrated that an unfamiliar person's locomotor synchronization with dogs' induces afterwards dogs' locomotor synchronization with the unfamiliar person's. Dogs are therefore sensitive to behavioural synchronization directed towards them (direct sensitivity). However, dogs often encounter unfamiliar people in the presence of their owner (Casey et al., 2014; Cornelissen and Hopster, 2010). Given that dogs are highly influenced by their owners' behaviours and are sensitive to human third-party interactions in certain contexts, it is crucial to investigate how the interaction between an unfamiliar person and dogs' owner affects the dogs' behavioural response towards the unfamiliar person in an ecological setting. That is why in the present study, we explored the effect of an unfamiliar person's behavioural synchronization with dogs' owners on dogs' behavioural synchronization with the unfamiliar person during a walk, a context never tested before. We used this ecological context because dogs appear to be sensitive to third-party interactions when the outcome of the interaction is visible or attractive to dogs, and going for a walk with their owner is a rewarding activity for dogs: it meets the dogs' energy expenditure needs and provides shared time with the human with whom they are most affiliated (Carlone et al., 2019; Curl et al., 2016; Cutt et al., 2008). Moreover, this study holds significant practical implications for enhancing the management of encounters between dogs and unfamiliar people during walks. According to Casey et al. (2014), 5% of dog owners report that their dog exhibit aggressive behaviours, such as threatening behaviours, biting or attempted biting, towards unfamiliar people in outdoor environments. Our research thus offers valuable insights for preventing problematic behaviours and fostering positive social interactions between dogs and humans in everyday situations.

In our experiment, during a first phase of 15 minutes, an unfamiliar person synchronized their locomotion with the owner's and talked with the owner for one experimental group (synchronization and communication with the owner (Sync and Talk)); for the other experimental group, the unfamiliar person stayed away from the owner and did not communicate with the latter (desynchronization and no communication with the owner (Desync and No Talk)). For both experimental groups, we analyzed the direction of the dogs' visual and olfactory attention during Phase 1. Next, as in Part 1 (Lamontagne et al., 2024), we compared the dogs' locomotor synchronization with the unfamiliar person's during a straight-line walk (Phase 2). We hypothesized that dogs would be sensitive to interactions between their owner and an unfamiliar person, and that there would be a more marked locomotor synchronization with the experimenter during the straight-line walk for dogs in the Sync and Talk group compared to dogs in the Desync and No Talk group. This would result in closer proximity to the experimenter and more time spent near the experimenter (location synchronization), a smaller difference between the dog's speed and the experimenter's speed and more time spent at a similar speed (activity synchronization), and more dogs adjusting their speed when the experimenter changed speed (temporal synchronization), for dogs in the Sync and Talk group compared to dogs in the Desync and No Talk group. Finally, we compared gazing behaviour between the two experimental groups and hypothesized that dogs in the Sync and Talk group would spend more time gazing at the experimenter and less time gazing at their owner than dogs in the Desync and No Talk group.

2. Material and methods

2.1. Ethical note

This experimental study was conducted in accordance with the Declaration of Helsinki and its latest revision in 2013, the legal requirements of France and the institutional guidelines of Aix-Marseille University. The ethics committee stated that this study was exempt from ethical approval because it was conducted in an unrestricted

outdoor environment without any physical constraints for the dogs. All owners who participated signed a consent form. All the dogs were in good health, and none showed signs of aging or behavioural problems, based on information from the owners and observations by the experimenter (a veterinarian). All the dogs were used to humans and were not fearful of unfamiliar people. They were all used to being walked off leash and wearing a harness. No physical restraint was imposed on the dogs during the experiment. They wore a Gopro® harness with a GPS and a Gopro® camera attached to it during the experiment, and they were given 10 minutes to get used to wearing the harness. During the experiment, none of the dogs exhibited any stress or fear signals. At the end of the experiment, all the dogs returned home with their owners.

2.2. Participants

Thirty-two dogs weighing at least 7 kg and from any breed or crossbreed participated in the study (dog breeds, identified based on information provided by owners when available, and visual inspection otherwise, are presented in Table 1 in the Supplemental File). Sample size was calculated beforehand on the basis of previous research using a similar protocol (Duranton et al., 2018; Lamontagne et al., 2023; Festing, 2018). The dogs were 1–11 years old (mean ± *SD* = 3.13 ± 2.25 years old; mean ± *SD* for dogs in the Sync and Talk group = 2.56 ± 1.79 years old; mean ± *SD* for dogs in the Desync and No Talk group = 3.69 ± 2.57 years old). Out of the 32 dogs, 20 were neutered (9 males and 11 females), and 12 were intact (7 males and 5 females). All dogs knew basic training commands (sit, down, come). Half of the dogs, counterbalanced for sex, were assigned to an experimental group with the unfamiliar person who interacted with the owner for 15 minutes. The other half of the dogs, counterbalanced for sex, were assigned to an experimental group with the unfamiliar person who did not interact with the owner for 15 minutes. None of the dogs participated in the Part 1 study (Lamontagne et al., 2024). As in the Part 1 study, owners were recruited voluntarily. We distributed posters in dog parks and posted calls for participation on social media platforms so that interested individuals could contact us.

2.3. Experimental procedure

Dogs were tested individually in an open outdoor space near Toulouse, France, comprising a grassy area of approximately 20 000 m^2. This open area was the identical to the one where dogs in the Part 1 study were observed. No one was present except the experimenter, playing the role of the unfamiliar person, and the owner. The dog was off leash and no instructions were given to the dog during the entire experimental procedure. We used the same cameras and GPS material as in the Part 1 study. When the owner and the dog arrived at the test site, the owner attached a harness with a GPS and a GoPro® camera on their dog's back. The dog was then given 10 minutes to freely explore the test site and get used to the equipment. During this time, the experimenter equipped the owner and themselves: each wore a harness with a GPS, and the experimenter briefly explained the experimental procedure to the owner. The experimenter and the owner each displayed a neutral facial expression during the whole experiment. The experimenter remained the same for all the dogs and was the same person as in the Part 1 study. The experiment took place in two phases:

2.3.1. Phase 1: 15 minutes of synchronization and communication or desynchronization and no communication with the owner (Fig. 1.A)

When the dog had finished exploring, the experimenter called the dog to join them, turned on the 3 GPS devices and then observed the dog in one of the two experimental groups: for the synchronization and communication with the owner (Sync and Talk) group, the experimenter and the owner spent 15 minutes in close proximity of each other, talking and walking around the test area together: for the desynchronization and no communication with the owner (Desync and No Talk) group, the experimenter and the owner spent 15 minutes in the test area at the same time, walking on their own; the experimenter stayed away from the owner and did not speak to the owner. In each of the experimental groups, the experimenter filmed the dog with a hand-held camera, they did not look directly at the dog but observed the dog through the camera's feed. The owner did not look at or talk to the dog, except in the following case: the owner called the dog's name once if the dog was about to exceed the limits of the test area. As in the Part 1 study, we implemented rules to keep the dogs active and maintain their attention on the experimenter: if the dog did not look at the experimenter for 1 minute, or if the dog was inactive for 1 minute, the experimenter called the dog's name, and if the dog was still inactive after 2 minutes, the experimenter indicated to the owner to say the dog's name.

2.3.2. Phase 2: 45 second straight-line walk (Fig. 1.B)

After Phase 1, the owner went to a position indicated by the experimenter, in full view of the dog, and remained there until the end of the test. The procedure of Phase 2 of the current experiment was then strictly identical to that of Phase 2 in the Part 1 study (Lamontagne et al., 2024): the experimenter turned on the GoPro® camera attached to the dog's harness and two cameras installed on tripods. The experimenter then went to the starting point of the straight-line walk and called the dog. This approach ensured that all the dogs were at the same distance from the experimenter at the beginning of the straight-line walk. After a ten-second countdown, the experimenter walked in a straight line in the three speed conditions (static, slow walk and fast walk) in a randomly assigned order without a break between them. In the static condition, the experimenter stayed still for 15 seconds. In the slow-walk condition, the experimenter walked slowly in a straight line for 15 seconds. In the fast-walk condition, the experimenter walked quickly in a straight line for 15 seconds. Neither the experimenter nor the owner looked at or talked to the dog during the straight-line walk. The experimenter used their phone as a timer and wore headphones to prevent the sounds signaling speed changes from being audible to the dogs.

2.4. Data analysis

2.4.1. Phase 1

During the 15-minute phase of synchronization and communication or desynchronization and no communication with the owner, we first checked that the mean distance between the experimenter and the owner was smaller for dogs in the Sync and Talk group compared to dogs in the Desync and No Talk group. This would confirm that the experimenter correctly synchronized and desynchronized with the owner's locomotion. We also compared the mean distance between the experimenter and the dog and the mean distance between the dog and the owner between the two experimental groups.

We then analyzed the dogs' behaviour in terms of the following variables using GPS data and video recordings: gaze at the experimenter, proximity to the owner, visual attention to an element other than the experimenter, olfactive attention, and motor inactivity. The definition of each of these variables is provided in Table 1. We performed ANOVA to analyze dogs' behavioural responses, with experimental group (2 levels: synchronization and communication with the owner (Sync and Talk) and desynchronization and no communication with the owner (Desync and No Talk)) as a between-subject factor and the dog's sex (2 levels: male and female) and age (2 levels: young adult, i.e. between 1 and 2 years old, and mature adult, i.e. over 2 years old, based on the classification proposed by Harvey 2021) as control predictors.

2.4.2. Phase 2

During the straight-line walk, we analyzed dogs' locomotor synchronization with the experimenter, gazing behaviour, and social attraction to their owner. The definition of each of the dependent variables is provided in Table 2. The statistical analyses of these variables are identical to those conducted for Phase 2 of the Part 1 study (see the

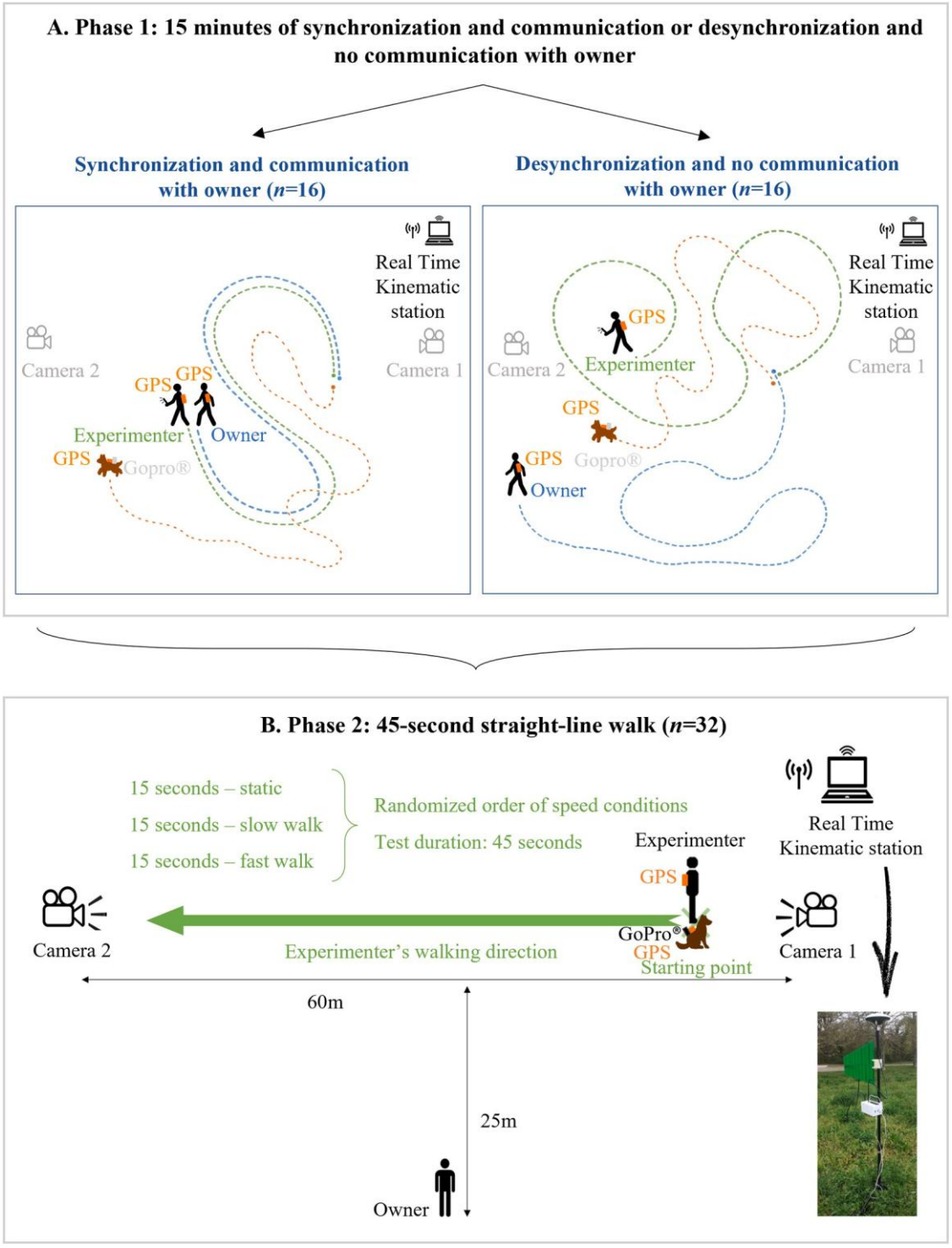


Fig. 1. Experimental procedure. A. Each dog was assigned to one of the two experimental groups. B. After the 15 minutes of synchronizing and talking or desynchronizing and not talking with the owner, the experimenter walked for 45 seconds in a straight line at three different speeds (static, slow walk and fast walk).

Data Analysis section of Phase 2 variables in the Supplemental File). A blind coder coded the variables from the video recordings using Media Player Classic Home Cinema software (version 1.7.13, https://mpc-hc.org). A second coder who was unaware of the hypotheses independently coded a randomly selected subset of 25% of the data. They were trained prior to the coding. We used videos from previous studies as references for their training. They coded these videos and their coding was compared to the reference coding. They continued coding training videos until their results aligned with the reference results. Once their coding perfectly matched the reference coding, they proceeded to code the videos of the Part 1 and Part 2 studies. The inter-rater reliability was assessed by Pearson's correlations. A high level of agreement between raters was found for all the variables (Phase 1: gaze towards the experimenter: $r = 0.95$, $p < 0.001$; visual attention to an element other than the experimenter: $r = 0.98$, $P < 0.001$; olfactive attention: $r = 0.98$, $P < 0.001$; motor inactivity: $r = 0.95$, $P < 0.001$; Phase 2: latency: $r = 0.97$, $P < 0.001$; gaze towards the experimenter: $r = 0.97$, $P < 0.001$; gaze towards the owner: $r = 0.98$, $P < 0.001$; time before going to the

Table 1
Definitions of the dependent variables studied in Phase 1.

Dependent variable	Definition
Gaze at experimenter	Time in seconds spent with the dog's nose oriented towards the camera held by the experimenter.
Proximity to owner	Time in seconds that the dog spent less than one metre from the owner, from GPS data.
Visual attention to element other than experimenter	Time in seconds that the dog spent static, with body in tension, head straight and gaze fixed and not directed towards the experimenter, from video recordings.
Olfactive attention	Time in seconds that the dog spent motionless or moving very slowly and with muzzle on the ground, from video recordings.
Motor inactivity	Time in seconds that the dog spent sitting or lying down, without engaging in visual, olfactory or auditory attention, from video recordings.

owner: $r = 0.99$, $P < 0.001$). The coders also examined the experimenter's behaviours; the aim was to confirm that the experimenter behaved consistently with all the dogs during the straight-line walk. We verified that the experimenter followed the speed conditions during the straight-line walk using a Linear Mixed Model (LMM): we modelled the experimenter's speed as a function of the speed condition, experimental group and the interaction between these factors as fixed effects. We included dog participants as random effects and an autocorrelation structure of order 1.

Since the straight-line walking phase was identical in the Part 1 and Part 2 studies, and the same variables were analyzed, we were able to directly compare the two experiments. Consequently, we tested the effect of the experimental procedure (Part 1: synchronization with the dog and Part 2: synchronization with the owner) on the dogs' behavioural synchronization and gaze activity towards the unfamiliar person using LMM, as well as on the dogs' social attraction towards their owner using ANOVA.

3. Results

3.1. Phase 1

3.1.1. Mean distances between dog, owner, and experimenter

Using GPS data, we calculated the mean distance between the experimenter and the dog, the mean distance between the dog and the owner and the mean distance between the experimenter and the owner during Phase 1. A Student t-test confirmed that the experimental procedure was respected, as the mean distance between the experimenter and the owner was shorter for dogs in the Sync and Talk group compared to dogs in the Desync and No Talk group (see Table 3, $t_{15} = 17.82$, $P < 0.001$, Cohen's $d = 6.30$). The mean distance between the dog and the owner did not differ between the two experimental groups ($t_{29} = 0.52$, $P = 0.608$). The mean distance between the dog and the experimenter was over 10 m for both experimental groups and was greater for dogs the Desync and No Talk group compared to dogs in the Sync and Talk group ($t_{21} = 3.70$, $P = 0.001$, Cohen's $d = 1.31$).

3.1.2. Dog behaviours

Dogs' behaviours were recorded during the 15-minute phase of synchronization and communication or desynchronization and no communication with the owner. ANOVA results are reported in Table 2 in the Supplemental File. The time the dogs spent gazing at the experimenter differed between the two experimental groups ($F_{1,28} = 12.34$, $P = 0.002$, Cohen's $d = 1.13$): dogs in the Sync and Talk group spent less time gazing at the experimenter than dogs in the Desync and No Talk group (Fig. 2). There was no effect of experimental group on dog

Table 2
Definitions of the dependent variables studied in Phase 2 and associated independent variables.

	Dependent variable	Definition	Independent variables
Location synchronization	Distance between dog and experimenter	Distance in metres between the experimenter and the dog. Calculated every 0.25 seconds from GPS data.	Experimental group Speed condition Straight-line walk period
	Time spent near experimenter	From GPS data, time in seconds that the dog spent within 5 m of the experimenter. Three values per dog calculated from GPS data.	Experimental group Speed condition Straight-line walk period
Activity synchronization	Speed difference	Absolute difference in metres per second between the experimenter's speed and the dog's speed. Calculated every 0.25 seconds from GPS data.	Experimental group Speed condition Straight-line walk period
	Time spent at a similar speed	Time in seconds during which the speed difference was less than 0.5 m per second. Three values per dog, calculated from GPS data.	Experimental group Speed condition Straight-line walk period
Temporal synchronization	Latency	If applicable, time the dog took to change speed after the experimenter changed speed. Two values maximum per dog, calculated from GPS data and video recordings.	Experimental group
Gazing behaviour	Gaze towards experimenter	Time in seconds spent with the dog's nose oriented towards the experimenter. Three values per dog, calculated from video recordings.	Experimental group Speed condition Straight-line walk period
	Gaze towards owner	Time in seconds spent with the dog's nose oriented towards the owner. Three values per dog, calculated from video recordings.	Experimental group Speed condition Straight-line walk period
Social attraction to owner	Time before going to owner	If present, length of time in seconds between the beginning of the straight-line walk and the moment when the dog arrived at the owner's feet, which were visible in the Gopro® camera's field.	Experimental group

Table 3
Mean distance between experimenter and owner, dog and owner, and dog and experimenter according to experimental group. Data are presented as mean ± *SD*.

	Experimental group	
	Synchronization and communication with the owner (Sync and Talk)	Desynchronization and no communication with the owner (Desync and No Talk)
Mean distance between the experimenter and the owner in metres	1.30 ± 0.31	21.43 ± 4.51
Mean distance between the dog and the owner in metres	14.66 ± 11.04	16.49 ± 8.93
Mean distance between the dog and the experimenter in metres	14.59 ± 10.98	25.81 ± 5.18

proximity to the owner, visual attention to an element other than the experimenter, olfactive attention or motor inactivity (see Table 2 in the Supplemental File). We established rules to prevent the dogs from remaining inactive for extended periods and to keep the dog's attention focused on the experimenter, but these rules were ultimately not used, as dogs did not spend more than one minute without looking at the experimenter, and no dogs were motionless more than one minute.

3.2. Phase 2

3.2.1. Dog locomotor synchronization, gazing behaviour, and social attraction

3.2.1.1. Experimenter's compliance to the experimental protocol. Naive coders' visual inspection confirmed that during the straight-line walk, the experimenter behaved consistently with all dogs: they looked at their phone and never turned their head throughout the entire walk, maintained a neutral facial expression, and remained silent. The analysis of the experimenter's speed data obtained from GPS data further confirmed that the experimenter complied with the speed conditions (χ^2_2 =521.45, $P < 0.001$; post-hoc tests: fast walk-slow walk: estimate ± SE = 0.45 ± 0.05, t_{60} = 8.66, P <0.001, Cohen's d = 1.28; fast walk-static: estimate ± SE = 1.16 ± 0.05, t_{60} = 22.63, P <0.001, Cohen's d = 3.34; slow walk-static: estimate ± SE = 0.72 ± 0.05, t_{60} = 13.97, P <0.001, Cohen's d = 2.06), with no differences between the two experimental groups (χ^2_1 = 0.81, P = 0.369).

3.2.2. Location synchronization

We measured the distance between the dog and the experimenter and the time the dog spent close to the experimenter during the straight-line walk. The full LMM results are reported in Table 3 in the Supplemental File. We found an effect of experimental group on the two variables (LMM of the distance between the dog and the experimenter: $\chi2_1$ = 18.76, $P < 0.001$, Cohen's d = 1.01; LMM of the time spent near the experimenter: $\chi2_1$ = 21.10, $P < 0.001$, Cohen's d = 1.59). The dogs in the Sync and Talk group were closer to the experimenter (Fig. 3.A) and spent more time near the experimenter (Fig. 3.B) compared to the dogs in the Desync and No Talk group. We also found an effect of straight-line walk period on these two variables (LMM of the distance between the dog and the experimenter: $\chi2_2$ = 23.43, $P < 0.001$; post-hoc tests: first period – second period: estimate ± SE = —7.23 ± 2.60, t_{48} = —2.78, P = 0.021, Cohen's d = —0.80; first period – third period: estimate ± SE = —12.29 ± 2.54, t_{48} = —4.84, $P < 0.001$, Cohen's d = —1.35; second period – third period: estimate ± SE = —5.06 ± 2.45, t_{48} = —2.07, P = 0.107, Cohen's d = —0.56; LMM of the time spent near the experimenter: $\chi2_2$ = 55.37, $P < 0.001$; post-hoc tests: first period – second period: estimate ± SE = 5.48 ± 0.96, t_{48} = 5.69, $P < 0.001$, Cohen's d =1.69; first period – third period: estimate ± SE = 6.68 ± 0.94, t_{48} = 7.14, $P <$ 0.001, Cohen's d =2.06; second period – third period: estimate ± SE = 1.20 ± 0.90, t_{48} = 1.33, P = 0.384, Cohen's d =0.37). For all the dogs, the distance between the dog and the experimenter increased over the course of the test (Fig. 3.A), so the time spent near the experimenter decreased during the test (Fig. 3.B). Speed condition did not affect the distance between the dog and the experimenter (see Table 3 in the Supplemental File) but did affect the time spent near the experimenter (LMM: $\chi2_2$ = 8.70, P = 0.013; post-hoc tests: fast walk – slow walk: estimate ± SE = —2.40 ± 0.93, t_{48} = —2.58, P = 0.034, Cohen's d = —0.74; fast walk – static: estimate ± SE = —2.36 ± 0.94, t_{48} = —2.52, P = 0.040, Cohen's d =-0.73; slow walk-static: estimate ± SE = 0.04 ± 0.94, t_{48} = 0.05, P = 0.999, Cohen's d =0.01). Dogs spent less time near the experimenter in the fast-walk condition (mean ± SD = 2.88 s ± 1.73 s) compared to the slow-walk (mean ± SD = 5.71 s ± 1.95 s) and static (mean ± SD = 3.56 s ± 2.07 s) conditions.

3.2.3. Activity synchronization

We analyzed the speed difference and the time spent at a similar speed during the straight-line walk. The full LMM results are reported in Table 4 in the Supplemental File.

There was an effect of speed conditions on the speed difference (LMM: $\chi2_2$ = 6.14, P = 0.046). Post-hoc tests yielded the following results: fast walk – slow walk: estimate ± SE = 0.30 ± 0.15, t_{48} = 2.62, P = 0.110, Cohen's d = 0.39; fast walk – static: estimate ± SE = 0.33 ± 0.15, t_{48} = 2.22, P = 0.078, Cohen's d =0.42; slow walk – static: estimate ± SE = 0.03 ± 0.15, t_{48} = 0.18, P = 0.982, Cohen's d = 0.03). Speed difference tended to be smaller in the static condition (mean ± SD = 0.66 ±

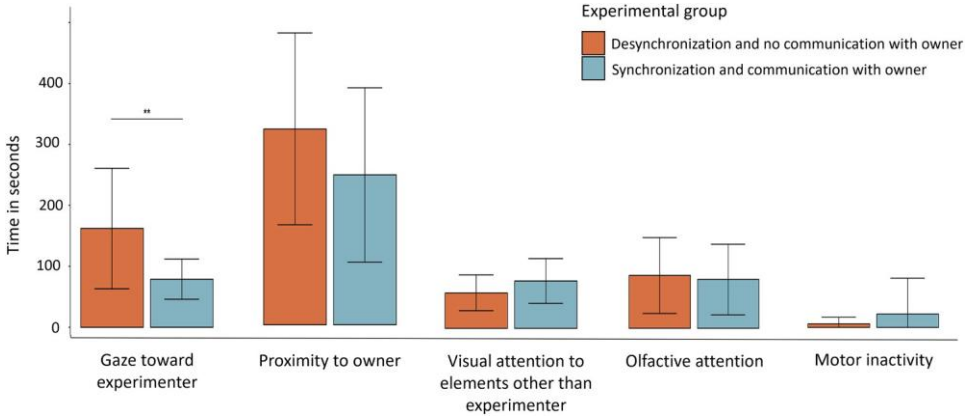


Fig. 2. Dog behaviours for each experimental group during Phase 1. Data are presented as mean ± *SD*. ** 0.001 < $P \leqslant$ 0.01.

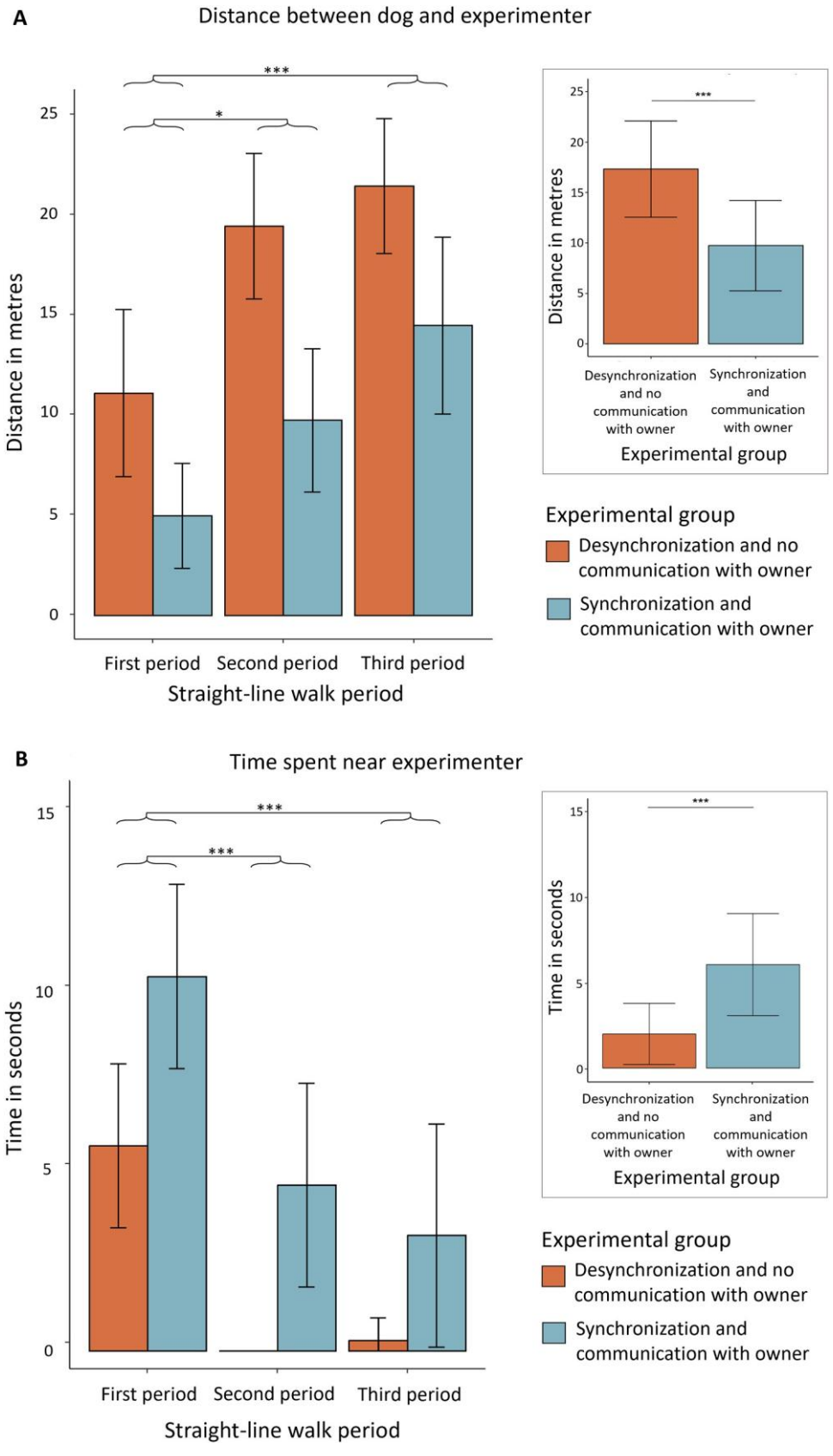


Fig. 3. Effect of experimental group and straight-line walk period on the distance between the dog and the experimenter (A) and on the time spent by the dog near the experimenter (B). Data are presented as mean ± *SD*. * $0.01 < P \leqslant 0.05$, *** $P \leqslant 0.001$.

0.91 m/s) compared to the fast-walk condition (mean ± SD = 1.00 ± 0.47 m/s). There was also a significant interaction between experimental group and straight-line walk period (LMM: $\chi 2_2$ = 7.15, P = 0.028). Post-hoc tests (see Table 5 in the Supplemental File) indicated that during the first period of the straight-line walk, speed difference was smaller for dogs in the Sync and Talk group compared to dogs in the Desync and No Talk group (Fig. 4).

No effect of experimental group or straight-line walk period was found on the time the dog spent at a similar speed to that of the experimenter (see Table 4 in the Supplemental File). There was an effect of speed condition, however (LMM: $\chi 2_2$ = 34.97, $P < 0.001$). Post-hoc tests yielded the following results: fast walk – slow walk: estimate ± SE = —2.24 ± 1.07, t_{48} = —2.09, P = 0.103, Cohen's d = —2.19; fast walk – static: estimate ± SE = —6.32 ± 1.08, t_{48} = —5.85, $P < 0.001$, Cohen's d = —6.18; slow walk – static: estimate ± SE = —4.08 ± 1.08, t_{48} = —3.77, P = 0.001, Cohen's d = —3.99. Dogs spent less time at a similar speed to that of the experimenter in the fast-walk (mean ± SD = 2.63 s ± 3.45 s) and slow-walk (mean ± SD = 4.38 s ± 3.80 s) conditions compared to the static condition (mean ± SD = 8.34 s ± 4.81 s).

3.2.4. Temporal synchronization

Thirteen out of 32 dogs adjusted their speed when the experimenter changed speed. The proportion of dogs who adjusted their speed was greater in the Sync and Talk group compared to the Desync and No Talk group (Fig. 5, $\chi 2_1$ = 4.66, P = 0.015). Dogs who exhibited latencies adjusted their speed in 2.16 s ± 1.94 s, with no effect of experimental group (see full LMM results in Table 6 in the Supplemental File).

3.2.5. Gazing behaviour

Dogs spent 3.41 ± 3.58 s per straight-line walk period gazing at the experimenter and 3.86 ± 3.99 s per straight-line walk period gazing at the owner; these variables were not affected by experimental group or speed condition (see full LMM results in Table 7 in the Supplemental File). Straight-line walk period did not affect the time spent gazing at the experimenter but did affect the time spent gazing at the owner (see Table 7 in the Supplemental File). Post-hoc tests yielded the following results: first period – second period: estimate ± SE = 2.47 ± 0.97, t_{48} = 2.54, P = 0.038, Cohen's d = —0.41; first period – third period: estimate ± SE = 4.02 ± 0.95, t_{48} = 4.25, $P < 0.001$, Cohen's d =-0.87; second period – third period: estimate ± SE = 1.55 ± 0.91, t_{48} = 1.71, P = 0.213, Cohen's d = —0.46). Dogs spent more time gazing at their owner during the first period of the test (mean ± SD = 6.22 s ± 4.44 s) compared to the second (mean ± SD = 3.19 s ± 3.26 s) and third (mean ± SD = 2.18 s ± 2.04 s) periods of the test.

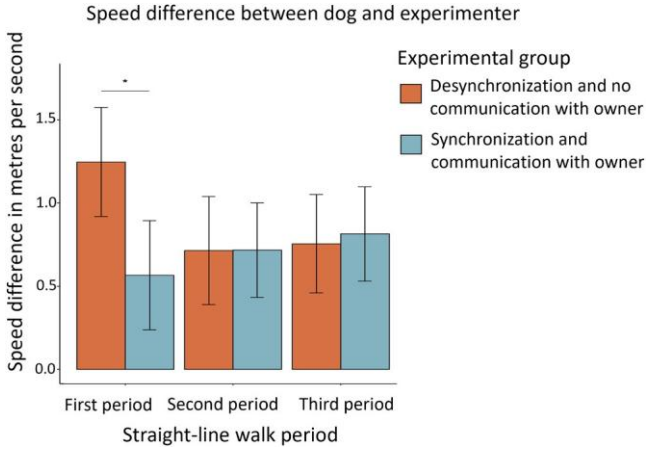


Fig. 4. Speed difference during the straight-line walk for the two experimental groups. Data are presented as mean ± *SD*. * $P \leqslant 0.05$.

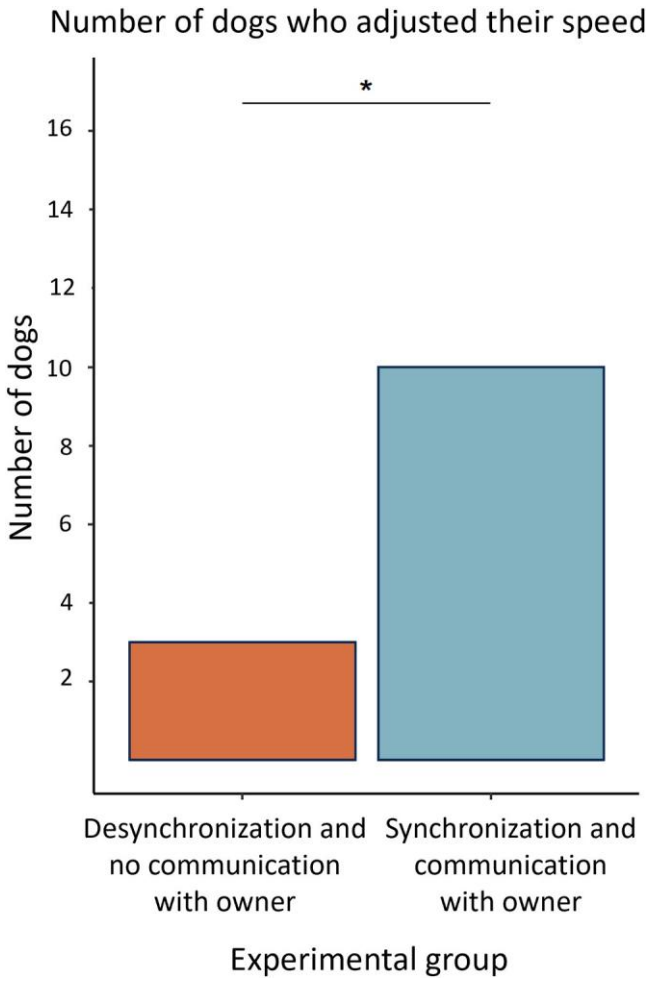


Fig. 5. Number of dogs who adjusted their speed when the experimenter changed speed, for the two experimental groups.

3.2.6. Social attraction

Sixteen dogs went to their owner before the end of the straight-line walk. The proportion of dogs who went to their owner did not differ between the two experimental groups, $\chi 2_1$ = 0.13, P = 0.362. Dogs who went to their owner did so in 17.59 s ± 10.45 s, with no effect of experimental group (see ANOVA results in Table 8 in the Supplemental File).

3.2.7. Direct comparison of Part 1 and Part 2 studies

We directly compared data from the Part 1 and Part 2 studies. We did not find any significant differences between the two studies regarding dogs' behavioural synchronization and gaze activity towards the unfamiliar person and dogs' social attraction towards their owner (see Table 4).

4. Discussion

We explored in this study the dogs' sensitivity to interactions between their owner and an unfamiliar person within a relevant ecological context, as off leash walks are an everyday activity for dogs and their owners. Specifically, we hypothesized that the interaction between the unfamiliar person and the dog's owner, which involved synchronizing and talking to each other, would subsequently induce the dog's behavioural synchronization with the unfamiliar person. This experiment was a challenge since dogs' indirect sensitivity had never been tested in a dynamic interaction between third parties nor in a task not involving food. Previous studies indicated that dogs' social and food preferences

Table 4
Direct comparison: Synchronizing with the dog (Part 1) vs synchronizing with the owner (Part 2).

	Dependent variable	$\chi 2$	*df*	*P*
Location synchronization	Distance between dog and experimenter	0.93	1	0.335
	Time spent near experimenter	1.01	1	0.315
Activity synchronization	Speed difference	1.56	1	0.212
	Time spent a similar speed	0.20	1	0.652
Temporal synchronization	Latency	0.06	1	0.808
Gaze behaviour	Gaze towards experimenter	1.54	1	0.214
	Gaze towards owner	1.62	1	0.203
		F	*df*	*P*
Social attraction to owner	Time taken to join owner	4.02	1	0.073

are sensitive to interactions between their owner and an unfamiliar person '(Freidin et al., 2013; Marshall-Pescini et al., 2011; Rooney and Bradshaw, 2006). Our study extends these findings and provides novel insights, by revealing for the first time that dogs' sensitivity to interactions between their owner and an unfamiliar person affects their locomotor response towards the unfamiliar person. Our study thus adds ecological validity and reinforces the external applicability of'dogs' sensitivity to human third-party interactions.

The interaction between the owner and the unfamiliar person subsequently affected the three components of the dogs' behavioural synchronization with the unfamiliar person during the straight-line walk. In other words, dogs synchronized their locomotion more with the experimenter's if the latter had walked and talked with their owners than if they had stayed away from their owners. More precisely, dogs in the synchronization and communication with the owner (Sync and talk) group stayed closer and spent more time near the experimenter (location synchronization) and had a smaller speed difference from that of the experimenter's at the beginning of the straight-line walk (activity synchronization) than dogs in the desynchronization and no communication with the owner (Desync and No Talk) group. In addition, more dogs in the Sync and Talk group adjusted their speed when the experimenter changed speed (temporal synchronization) compared to the dogs in the second experimental group. It should be noted that during the first phase, the mean distance between the dog and the experimenter was greater for dogs the Desync and No Talk group compared to dogs in the Sync and Talk group. However, the mean distance was greater than 10 m for both experimental groups, indicating that the differences between the two experimental groups during the straight-line walk are unlikely to be due to the difference in the mean distance between the dog and the experimenter during Phase 1. The three components of behavioural synchronization differed between the two experimental groups, but there was no difference between the two experimental groups regarding dogs' gazing behaviour towards the experimenter. However, dogs spent more time gazing at their owner at the beginning of the straight-line walk than at the end. During walks, dogs do not look at their owner often unless they encounter situations of uncertainty (Mongillo et al., 2014); in our study, the owners were walking and then suddenly stopped. Although the straight-line walk started a few minutes after the owner stopped walking, given that dogs are particularly attentive to their owner's actions (Horn et al., 2012; Mongillo et al., 2010; Schwab and Huber, 2006), it is possible that dogs gazed at their owner more at the beginning of the walk because they were seeking information about their owner's next action.

Importantly, another effect occurred during the straight-line walk: some dogs, regardless of the experimental group, moved away from the experimenter over the course of the straight-line walk, and the difference between the dog's speed and the experimenter's speed no longer differed between the two experimental groups after the first period of the straight-line walk. The GPS trajectories showed that dogs moved in the direction of their owners. This was due to the 'owner attractor' effect: dogs go to their owner first when in the presence of their owner and an unfamiliar person (Feuerbacher and Wynne, 2017; Palmer and Custance, 2008), and dogs tend to alternate between moving away from their owners and returning to them during walks (Foltin, 2021; Lamontagne et al., 2023). Interestingly, the proportion of dogs who went to their owners and the time before they went to their owners in our study did not significantly differ between the two experimental groups. Walking and talking with the owners thus temporarily enhanced dogs' behavioural synchronization with the unfamiliar person, but did not affect their social attraction to their owners.

Dogs typically do not synchronize with unfamiliar people. Our study is the first to reveal the possibility of dogs' behavioural synchronization with unfamiliar people when those people exhibit specific behaviours towards dogs' owner. A question arises as to the cognitive mechanisms underlying this behavioural synchronization. Dogs' behavioural alignment with the unfamiliar person may stem from an automatic process of execution of the perceived action, the dogs reproducing the behaviour they observed for 15 minutes. In humans, perception and execution of actions share a common neural network. There is thus an action perception coupling, making observers more likely to execute the action they observe. This action perception coupling leads to motor contagion, when individuals copy the behaviour they perceive (Blakemore and Frith, 2005). A similar process may be present in dog-human interactions: dogs perceive the two human agents synchronizing with each other and it makes dogs more likely to synchronize with the unfamiliar person. Motor contagion has been widely studied at the intraspecific level (see Lamontagne and Gaunet, 2023 for a review). Our study is thus the first to suggest motor contagion at the interspecific level when dogs perceive behaviours performed by two humans.

It is noteworthy that the owners were involved in the 15-minute interaction between humans. Owners are dogs' social reference (Mariti et al., 2013), so dogs may have aligned their behaviour with that of the unfamiliar person during the straight-line walk because through social referencing, they copied the behaviour performed by their owner towards the unfamiliar person during the 15 minutes (Duranton et al., 2016; Merola et al., 2012a, 2012b). Moreover, dogs in Desync and No Talk group spent more time gazing at the experimenter than dogs in the Sync and Talk group during the 15 minutes, and a previous study showed that during an encounter with an unfamiliar person, dogs looked at the unfamiliar person earlier if the owner retreated than if the owner approached the unfamiliar person (Duranton et al., 2016). These results indicate that dogs used their owners' behaviours and were looking for social cues from the unfamiliar person if the person was not with the owner, suggesting that a person who is not accepted in the close surroundings of the owner must be visually monitored. Considering this, the dogs' indirect sensitivity to human interactions is possibly due to the involvement of the owner in the interaction, as suggested in an earlier study (Chijiiwa et al., 2015). If the unfamiliar person was with the owner, their behaviour could be more predictable for the dogs. Consequently, the dogs would require less monitoring of the unfamiliar person's behaviours, and the unfamiliar person would indirectly become familiar with the dogs by interacting with their owners. This highlights a process of transitivity of familiarity: their owners' friends are dogs' friends. The two mechanisms are not mutually exclusive, as the dogs may align with the experimenter during the straight-line walk due to both an automatic process and a transitivity of familiarity. Additional studies, particularly replicating the protocol with two individuals unfamiliar to the dogs, are essential to determine if behavioural alignment with an unfamiliar person can occur when the owners are not involved in the human interactions. If confirmed, this would evidence the existence of an automatic process triggered when dogs perceive interactions between two humans. Otherwise, it would mean that alignment with an unfamiliar person may only occur when a familiar person is involved in the human interactions.

The statistical comparison of our two studies (Parts 1 and 2) indicates that dogs' perception of the unfamiliar person's behavioural

synchronization with them or with their owner induces in both cases the dog's behavioural synchronization with the unfamiliar person (see Table 4). Interestingly, however, the effects of direct and indirect sensitivity on dogs' behavioural response slightly differ in terms of dogs' social attraction to the owner (see Table 4): the dogs who went to their owner did so later when the unfamiliar person had previously synchronized their locomotion with the dogs' (33.36 ± 2.02 s) than when they had previously synchronized their locomotion with that of the dogs' owners (21.30 ± 4.82 s). In summary, directly synchronizing with the dogs or their owners has the same effect on the dogs' behavioural response, but this response lasts longer when the synchronization is directed towards the dogs than towards the owner. In other words, aligning one's behaviour with that of a dog is more efficient than aligning it with the behaviour of the dog's owner. It is worth noting that in both studies, we implemented rules to keep the dog active and maintain their attention on the experimenter. While the rule to maintain the dog's attention focused on the experimenter was unnecessary in both studies, the rule to keep the dog active was necessary for 17 dogs in the Part 1 study but not for any dogs in the Part 2 study. This difference is not surprising, given that the owners in the Part 1 study remained stationary during the 15-minute observation phase, whereas owners in the Part 2 study were moving during the 15-minute observation phase, and dogs tend to synchronize their behaviour with that of their owner. We cannot rule out the possibility that the difference in the results between the two experiments may be partly attributed to the fact that the experimenter called the dog's name for some dogs in the Part 1 study, but did not do so for any dogs in the Part 2 study.

Our work brings new insights into dogs' behavioural synchronization with humans. Previous studies showed that dogs synchronize their behaviour with that of their owner but not with that of unfamiliar people (Duranton et al., 2016, 2017b, 2019). For the first time, our study reveals that dogs can exhibit behavioural synchronization with an unfamiliar person if the person has interacted for a short period with the owner beforehand, but interacting with the owner does not affect the attractor effect of the owner afterwards. Our findings are of interest in the management of dogs in daily life, as dog-owner dyads regularly encounter unfamiliar people (Casey et al., 2014; Cornelissen and Hopster, 2010). For example, during a veterinary consultation, health care procedures are carried out with reduced stress and physical restraint for dogs if the staff take the time to talk with owners before interacting with their dogs (Girault et al., 2022; Helsly et al., 2022). As another example, if a new pet-sitter spends time with the owner first, the dog will be more likely to synchronize with the pet-sitter afterwards during walks, thus limiting the risk of the dog running away or producing agonistic behaviour. Finally, this study involved dogs that are not fearful or aggressive towards unfamiliar people, but our findings could likely be extended to dogs reactive to unfamiliar people. The protocol could be adapted and used in behaviour modification procedures: an unfamiliar person would walk with the owner without interacting with the dog. If the dogs then gradually copy human behaviour and synchronize with the unfamiliar person, this approach would hold promise for desensitizing and counter-conditioning reactive dogs during walks.

As a final point, like all experiments, this study has limitations. The constraints related to the testing area and the recruitment of dogs are the same as those of the Part 1 study. Furthermore, in both studies, dogs were free to move, requiring interaction between the experimenter and the dog before the straight-line walk to ensure all dogs were positioned near the experimenter just before the walk. Perhaps the dogs' behaviour would have differed if they had not been called by the experimenter. However, in such a scenario, it would have been challenging to compare the dogs' locomotor behaviour during the walk if they had started at varying distances from the experimenter. Additionally, during Phase 1 of this study, when the experimenter synchronized their locomotion with that of the owner, they also talked with the owner. We made this choice to create an ecologically valid setting, and it would be unusual for dogs to observe their owner walking with an unfamiliar person for an extended period without any verbal interaction. However, this approach leaves it unclear whether it was the act of walking together, conversing together, or both, that influenced dogs' behaviour afterwards. Finally, we recall that the owner was involved in the human interaction perceived by dogs in this study. Conducting a similar study in which the dogs observe an interaction between two unfamiliar people would establish the extent to which social referencing is involved in interspecific motor contagion. Investigating the potential extension of our findings to other dog populations, notably shelter dogs, also presents an intriguing avenue for research. If shelter dogs indeed exhibit enhanced synchronization with a new person when the person walks with a shelter caregiver during their initial encounter, this practice could be implemented in shelters, enhancing the chances of successful adoption by fostering positive interactions between shelter dogs and potential adopters.

5. Conclusion

We investigated dogs' eavesdropping, i.e. dog sensitivity to third party interactions, for the first time in an ecological setting and without food involvement, as it was in the context of a synchronous walk involving dogs' owner and an unfamiliar person in an outdoor environment. We revealed that talking and synchronizing with dogs' owner, characterized by the alignment of walking speed and the maintenance of a proximity of 1 m, significantly enhanced dogs' behavioural synchronization with the unfamiliar person. These results indicate that dogs reproduce the behaviours they perceive, through an automatic process of motor contagion, and/or through social referencing, the unfamiliar person indirectly becoming familiar to the dogs during their interaction with the dogs' owners. These insights hold practical significance, considering the frequent encounters between unfamiliar people and dog-owner dyads in daily life. Our study advocates for a strategic approach when engaging with such dyads, proposing an initial interaction with the owner while ignoring the dog. This facilitates subsequent interactions with the dog, and helps mitigate potential stress. Consequently, behavioural synchronization with the owner emerges as a valuable tool for adeptly managing encounters between unfamiliar people and dog-owner dyads, thereby contributing to an enhanced well-being for dogs during such interactions.

Author contributions

All authors contributed to the study conception and design. Material preparation and data collection and processing were carried out by Ang´elique Lamontagne and Thierry Legou. Statistical analyses were carried out by Ang´elique Lamontagne. The first draft of the manuscript was written by Ang´elique Lamontagne, and all authors commented on previous versions of the manuscript. All authors gave final approval for publication and agreed to be held accountable for the work.

Funding

This work was supported by the National Association for Research and Technology (ANRT), the association *Agir pour la Vie Animale*, the French National Centre for Scientific Research (CNRS), and Aix-Marseille University.

CRediT authorship contribution statement

Thierry Bedossa: Writing – review & editing, Supervision, Funding acquisition, Conceptualization. **Florence Gaunet:** Writing – review & editing, Supervision, Methodology, Funding acquisition, Conceptualization. **Ange´lique Lamontagne:** Writing – original draft, Methodology, Formal analysis, Data curation, Conceptualization. **Thierry Legou:** Writing – review & editing, Supervision, Methodology, Formal analysis, Data curation, Conceptualization.

Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Acknowledgements

The authors are grateful to the owners who volunteered for the study. The authors also thank Camille Valle and Gael Montredon for the coding of the video recordings.

Appendix A. Supporting information

Supplementary data associated with this article can be found in the online version at doi:10.1016/j.applanim.2024.106271.

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3. Modulation de la synchronisation comportementale chez le chien par le nombre d'agents humains

Nous avons exploré l'effet du nombre de personnes sur la synchronisation comportementale du chien sur l'humain. Une synchronisation du chien plus marquée lorsque le nombre d'humains augmente pourrait soutenir l'hypothèse de la résonance motrice interspécifique, car chez l'humain, la synchronisation comportementale augmente avec la taille du groupe, en raison d'une plus forte activité des neurones miroirs (Cracco et al., 2016, 2019). Dans une étude menée pendant mon Master 2, nous n'avions pas trouvé de différence significative sur le niveau de synchronisation locomotrice de chiens avec leurs propriétaires, que ces derniers marchent seuls ou avec deux autres personnes familières (Lamontagne et al., 2023). Nous avons reproduit le protocole de cette expérience, en supposant que le nombre de personnes module effectivement la synchronisation comportementale du chien sur l'humain, et que la différence entre une et trois personnes est peut-être trop subtile pour être perceptible. Dans ce protocole adapté, le groupe comprenait le propriétaire et 4 autres personnes, et nous avons ajouté une phase de séparation après la marche en ligne droite : le propriétaire se dirigeait seul d'un côté pendant que le reste du groupe allait de l'autre. Nous nous attendions à une plus forte synchronisation locomotrice des chiens sur leurs propriétaires pour les chiens avec le groupe par rapport aux chiens avec leur propriétaire seul, et à ce que les chiens suivent leur propriétaire plutôt que les 4 personnes lors de la séparation du groupe du fait de l'effet attracteur du propriétaire.

Nous n'avons finalement pas observé d'effet de groupe pendant la marche en ligne droite, contrairement à nos hypothèses. Cependant, pendant la séparation du groupe, les chiens avaient tendance à d'abord suivre les 4 personnes pendant environ 20 secondes, puis à rejoindre leur propriétaire.

A la lumière de ces résultats, il apparaît que le nombre de personnes influence bien l'alignement comportemental des chiens, sinon ils n'auraient pas eu tendance à suivre les 4 personnes au moment de la séparation du groupe. Il est probable que cet effet de groupe soit masqué par l'effet de l'affiliation avec le propriétaire pendant la marche en ligne droite. Par ailleurs, le fait que l'effet de groupe ne soit pas mis en évidence pendant la marche, et qu'il soit supplanté tardivement par l'effet d'affiliation lors de la séparation de groupe suggère que les effets de ces deux facteurs sur l'alignement comportemental des chiens soient sous-tendus par des processus cognitifs distincts. Cette étude ne pouvant pas déterminer les mécanismes cognitifs en question, j'examinerai ces résultats vis-à-vis de l'hypothèse de la résonance motrice interspécifique dans la discussion générale.

Article 4 : Lamontagne, A., Legou, T., Bedossa, T. & Gaunet. F. (accepted). Social modulation of dogs' behavioural synchronization with humans: Effect of number of people and owner's presence. *Animal Behaviour*.

Title: Social Modulation of Dogs' Behavioural Synchronization with Humans: Effect of Number of People and Owner's Presence

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Abstract

Dogs' behavioural synchronization with humans is well established, but few studies have examined its social modulation. We investigated whether the number of human agents modulates interspecific behavioural synchronization. We replicated the protocol of Lamontagne et al. (2023) comparing dogs' locomotor synchronization either with their owner alone (n = 20) or with the owner and four other people (n = 20) during a straight-line walking task and using GPS devices. Our results are consistent with those of the previous study and show no significant difference between the two experimental groups. Specifically, dogs stayed at an average distance of 5 m of their owner, they adjusted their speed to that of the humans' speed, and they adapted their speed within about 2 seconds when humans changed speed. To further explore the effect of the number of humans on dogs' behavioural alignment, the five-

person group separated at the end of the straight-line walk, with the owner going one way and the rest of the group the other. Fifteen out of 20 dogs followed the group after the separation and then went to their owner afterwards. We suggest that the number of agents modulated dogs' behavioural synchronization with humans, as dogs followed the group of humans, but this group effect was masked during the straight-line walk by another social modulator, namely the attracting effect of the owner due to the affiliation between the dogs and their owner.

Keywords

Affiliation, Behavioural synchronization, Canine, Group, Motor entrainment, Motor resonance, Social modulation

Highlights

- Dogs with their owner alone synchronize as much as dogs with a five-person group
- When the group splits, dogs followed the four-person group
- Group-following behaviour is then overridden by affiliation effect of the owner
- Affiliation and number of persons both modulate dogs' alignment with humans

INTRODUCTION

Dogs and humans share a unique relationship within the animal kingdom. Dogs were the first species to be domesticated and have shared an environment with humans for millennia (Charles, 2016). Today, dogs interact daily with humans right from their early days of life (Duranton et al., 2022). Dogs' acculturation into the human environment, coupled with artificial selection and their extremely early socialization with humans, has led to the development of particular social cognitive abilities in these canids (Topál et al., 2009; Range & Marshall-Pescini, 2022; Udell et al., 2016). Numerous studies have highlighted the sensitivity of dogs to human

behaviours, their ability to discern human attentional states, and their aptitude for referential communication with humans (see Bensky et al. 2013; Duranton & Gaunet, 2015; Siniscalchi et al., 2018; for reviews). Given these social cognitive abilities, dogs represent a promising model for studying behavioural copying at the interspecific level (Hare & Ferrans 2021; Topal et al. 2009). Behavioural copying, including notably automatic imitation, deferred imitation, overimitation and behavioural synchronization, is well documented across various social species at the intraspecific level and serves adaptive functions, such as social learning, cooperation and social bonding (see Lamontagne & Gaunet, 2023, Palagi & Cordoni, 2020 for reviews). Research has demonstrated that dogs can mimic human actions, particularly those of their owners (Fugazza et al. 2019; Kubinyi et al. 2003a; Range et al. 2011), even after delays ranging from a few minutes to a full day (Fugazza & Miklosi, 2014, Fugazza et al. 2016). Dogs can also replicate actions that are irrelevant to the completion of a task (Huber et al. 2018), although this overimitation ability is less pronounced with an unfamiliar person than with their owners (Huber et al. 2020), underscoring the importance of owners as social models for dogs. Behavioural synchronization, a form of behavioural copying crucial for cooperation and cohesion, has also been demonstrated between dogs and humans, with studies showing that dogs spontaneously synchronize their behaviour with that of their owners during walks (Duranton et al., 2018; Lamontagne et al., 2023; Wanser et al., 2021). These studies focused on a walking task because behavioural synchronization can easily be studied in this context as it spontaneously arises when individuals walk together (Felsberg & Rhea, 2021).

Recent research has explored the social modulation of dog behavioural synchronization with humans, revealing similarities with behavioural synchronization in humans with regards to the effects of familiarity (Duranton et al., 2018, 2019, 2022; Lamontagne et al., 2024a,b) and locomotor profile (Wanser et al., 2021), suggesting shared properties between interspecific (between dogs and humans) and intraspecific (within humans) behavioural synchronization.

However, findings are not consistent with those of human studies regarding the effect of the number of agents. Behavioural synchronization increases with group size in humans (Cracco & Brass, 2018a,b,c; Cracco et al., 2015, 2016, 2019; Gallup et al., 2012; Milgram et al., 1969), but Lamontagne et al. (2023) found that dogs walking with their owner and two other people looked more at their owner but exhibited a similar level of locomotor synchronization to their owner as dogs walking with their owner alone. Lamontagne et al. (2023) thus found an effect of the number of humans on dogs' visual attention but not on dogs' locomotion. In contrast, other studies have shown that the number of people does influence dogs' behaviour. Kubinyi et al. (2003b), for example, found that dogs repeatedly exposed to a diversion route at the end of their daily walk with their owner needed fewer repetitions to initiate the diversion when another familiar person accompanied the owner than when the owner was alone. Another study showed that dogs faced with two groups of humans of different sizes (5 vs 1, 4 vs 2 and 3 vs 2) tended to go to the larger group of humans compared to the smaller one (Nagasawa et al., 2020). Dogs' familiarity with humans affected this tendency: when dogs were familiar with people in the smaller group, they went to the larger group less often, suggesting that dogs use both familiarity with humans and majority cues when following groups.

Given the mixed results regarding the impact of the number of people on dogs' behavioural alignment, further investigation is warranted. The lack of group effect in Lamontagne et al. (2023) study could be attributed to the group size, which may not have been sufficient to elicit a noticeable effect. Also, this study involved only two types of breeds (shepherd dogs and molossoids), with tenuous breed effects, so it was not representative of all pet dog breeds. In addition, Nagasawa et al. (2020) study did not involve owners, and as mentioned earlier, owners are social models for dogs. Dogs indeed behave differently with their owner compared to other people (Horn et al., 2013; Huber et al., 2020; Kerepesi et al., 2015), they tend to follow owner's social cues rather than unknown person's cues (Cook et al. 2014), they prefer to interact with

their owner rather than other people (Feuerbacher & Wynne, 2014, 2017), and when presented with three people moving away from them— their owner, a familiar person, and an unfamiliar person— dogs tend to follow their owner (Kerepesi et al., 2015). However, no studies have yet explored whether dogs' affiliation with their owners outweighs the group effect, in other words whether dogs would follow their owner over a group of humans.

Investigating how dogs' behavioural responses are influenced by the number of people and the owner's presence offers valuable insights into how dogs process and react to human stimuli in various social contexts. This is particularly relevant since dogs are frequently exposed to groups of people, often in the presence of their owners. The objectives of the present study were 1) to assess whether group size modulates dogs' behavioural synchronization with humans and 2) to determine whether affiliation overrides the group effect. We therefore conducted a two-phase protocol based on previous studies, enabling us to contextualize our results within the framework of previous findings. In the first phase, we replicated the straight-line walking protocol of Lamontagne et al. (2023), but this time including dogs of any breed and comparing the dogs' locomotor synchronization to their owner for two experimental groups: dogs with their owner alone and dogs with their owner and four other people. No instructions were given to the dogs in order to observe their spontaneous behaviour. The humans walked in three different speeds in a row, in a random order: static, slow walk and fast walk. In the second phase, which involved only the dogs with their owner and four other people, the group of five humans separated at the end of the straight-line walk, with the owner going to one side and the rest of the group to the other. This phase, inspired by Nagasawa et al. (2020), was not part of the protocol of Lamontagne et al. (2023). However, Nagasawa et al. (2020) study was conducted in a closed 25m² room and involved a preliminary learning phase in which the dogs received a food reward when following a human, and food rewards were also provided during the test. Our study was devoid of food rewards and was designed to take place in a more

ecological context, as dogs were off-leashed, received no rewards or instructions, and the task involved an outdoor walk, reflecting as much as possible the conditions of everyday walks that dogs are accustomed to.

We hypothesized that the number of agents is a common modulator of behavioural synchronization in humans and behavioural synchronization between dogs and humans, as previous studies have shown an effect of number of people on dogs' behaviour. The effect of the group was surprisingly not evident in the locomotion of dogs walking with three people, we expected that this effect would be noticeable for dogs walking with a larger group. As in Lamontagne et al. (2023) study, we measured the three components of behavioural synchronization during the straight-line walk: location synchronization (being physically close at the same time), activity synchronization (exhibiting the same behaviour simultaneously) and temporal synchronization (changing behaviour simultaneously) along with dogs' gaze behaviour towards their owner. This approach was chosen to make our methodology directly comparable to that of Lamontagne et al. (2023). We therefore expected that our results to converge with those of Lamontagne et al. (2023) for dogs with their owner alone. We expected that dogs with their owner and four other people would exhibit more marked locomotor synchronization and gaze behaviour to their owner compared to dogs with their owner alone, notably through a closer distance between the dogs and their owner (location synchronization), a smaller difference between the dogs' speed and the humans' speed (activity synchronization), and more time spent gazing at their owner. We did not expect differences between the two experimental groups with regards to temporal synchronization, as Lamontagne et al. (2023) found that dogs adjusted their speed within about two seconds when humans changed speed, and it is unlikely that this latency could be further reduced.

Our second hypothesis was that the effect of affiliation is stronger than the effect of the group, given that previous studies have highlighted the role of owners as models for dogs, and have

shown that dogs are less likely to follow larger groups when familiar individuals are in smaller groups. We therefore expected that during the separation phase, when these two social factors are pitted against each other, the presence of the owner would override the group effect, so the dogs would follow their owner (the stimulus with the highest social value) rather than the four other humans (the largest stimulus).

MATERIALS & METHODS

Ethical note

This study was conducted in accordance with the Declaration of Helsinki and its latest revision in 2013, the legal requirements of France, and the institutional guidelines of Aix-Marseille University. The ethics committee stated that this study was exempt from ethical approval because it was conducted with privately owned pet dogs in an unrestricted outdoor environment and without any physical constraints for the dogs. All owners voluntarily participated and signed a consent form. All the dogs were in good health, and none showed signs of ageing or behavioural problems, based on information from the owners and observations by the experimenters. None of the dogs were fearful of unfamiliar people. During the experiment, no physical restraints were imposed on the dogs. Each dog wore a GoPro© harness with a GPS and a GoPro© camera attached to it, and they were given 10 minutes to get used to wearing the harness before the experiment began. During the experiment, none of the dogs exhibited any stress or fear signals. At the end of the experiment, all the dogs returned home with their owners.

Participants

Forty dogs with a minimal weight of 7kg and from any breed or crossbreed participated in the study. The list of breeds for each experimental group is provided in Table S1 in Supplemental File 1. Sample size was chosen beforehand, on the basis of previous research using a similar

protocol (Lamontagne et al., 2023, Festing, 2018). Dogs' breeds were assigned based on information provided by the owners when available, and visual inspection otherwise. Dogs were randomly assigned to one of the two experimental groups, with equal numbers of females and males in each group: 20 dogs were observed with their owner alone, and 20 other dogs were observed with their owner and four other people. In both experimental groups, the dogs were between the ages of 1 and 10 years (mean ± SD = 4.32 ± 2.27, mean ± SD for dogs with their owner alone = 4.61 ± 2.49, mean ± SD for dogs with their owner and four other people = 4.03 ± 2.09). All dogs knew basic commands (sit, come).

Material

We used Global Positioning System (GPS) receivers associated with a Real Time Kinematic (RTK) base station. The base station sent real-time corrections to GPS receivers. Each GPS device recorded the received GPS frames every 0.25s, including the time, location, and the quality of the RTK correction. With the corrections of the base station, we received GPS positions with an accuracy of a centimeter. The processing of these GPS frames received (4 per second) provided positional data in XY coordinates. In the Lamontagne et al. (2023) study, only the owner and the dog wore a GPS. In the present study, all the participants carried a GPS. For dogs who were tested with the group, this system allowed us to check that the humans in the group were all walking at the same speed and maintained the same distance between them throughout the test.

We also used two cameras mounted on a tripod and a GoPro© camera attached to the harness worn by the dogs.

Experimental procedure

All the dogs were tested individually in the same outdoor space, near Toulouse, France. The test site was identical to that of Lamontagne et al. (2024a,b) and consisted of an open area of grass, approximately 100 m by 200 m, totaling 20 000 m^2, ensuring unrestricted movement for the dogs. The participants spent approximately 45 minutes at the test site. The dogs were off leash during the entire procedure. The experiment took place over a period of six weeks. In a few cases, more than one dog participated in the experiment on the same day, but in those cases, the two observations were spaced out by several hours. The same four experimenters (E1, E2, E3, E4) were present during all of the procedures. Owners came alone with their dog for dogs tested with their owner alone, and they came with their dog and one accompanying person familiar to the dog (a member of the household, the owner's family or a friend who saw the dog every week) for dogs tested with their owner and four other people. The three other people accompanying the owner were the experimenters (E1, E2 and E3). We chose to include three experimenters in the group rather than three people previously familiar to the dog for recruitment reasons. Owners were recruited voluntarily through flyers distributed in dog parks and calls for participation on social media platforms, and it would have been challenging to recruit owners and four people familiar to the dog available for the experiment. However, we know from previous studies that an unknown person can become familiar to a dog in just 15 minutes by interacting with the dog or its owner (Feuerbacher & Wynne, 2017; Lamontagne et al., 2024a,b). Moreover, having the same three experimenters for all 20 dogs ensured less variability in the level of familiarity between the dogs and the members of the group.

E1, E2 and E3 spent 15 minutes becoming familiar with each dog and owner prior to the procedure: they interacted with the dog, playing with it and petting it, and talked with the owner. They also explained the protocol of the straight-line walk to the owner and the accompanying person if present. E4 did not interact with the dog but was there to ensure that the procedure was correctly conducted. After 15 minutes, E4 equipped the owner and the accompanying

person if present with a GPS harness, then the owner equipped the dog with the harness to which a GPS and a GoPro© camera were attached. The dog was given 10 minutes to get used to the equipment. E1, E2 and E3 also each wore a GPS harness. The protocol of the straight-line walk, identical to that of Lamontagne et al. (2023), then began. A video illustrating the experimental procedure is available in Supplemental File 2.

- Straight-line walk with the owner alone (n = 20) vs with the owner and four other people (n = 20)

E4 turned on the cameras and then hid behind an obstacle to avoid being a source of distraction for the dog (Fig.1a). The group went to the starting point of the straight-line walk and called the dog. The group first faced Camera 1, with the owner and the accompanying person next to each other and three experimenters behind them (Fig. 1a). The position of the owner in relation to the accompanying person (to the right or to the left) and the positions of E1, E2 and E3 in relation to each other were randomized. The five people simultaneously launched a web application that served as a timer. When the application was launched, an initial 10-second countdown started: during this preparation phase, the five people could communicate with each other and with the dog. At the end of the 10 seconds, a sound signal was emitted, indicating to the humans to stop communicating with each other and with the dog, turn 180 degrees, and start walking in the first speed condition. In this way, the owner and the accompanying person were behind the three experimenters during the walk (Fig.1b). We chose to split the group into two lines, as it reflects the typical behaviour observed among groups during pedestrian movements (Moussaïd et al., 2010; Zanlungo et al., 2017), so this configuration was not unusual for the dogs. Also, dogs usually walk in front of humans during walks, so we positioned the owner behind the experimenters during the walk to ensure that the dogs could see the entire group and not just focus on their owner. The group maintained this configuration throughout the test, and the members of the group were asked to coordinate their walking pace. They walked in the three

speed conditions in a random order. In the static condition, they stayed still for 15 seconds. In the slow-walk condition, they walked slowly in a straight line for 15 seconds. In the fast-walk condition, they walked quickly in a straight line for 15 seconds. A sound signal was emitted every 15 seconds to indicate to them to change their speed. They wore headphones so that the sound signals could not be heard by the dogs. As they had launched the application simultaneously, each of them heard the sound at the same time and changed speed simultaneously.

For dogs tested with their owner alone, E4 turned on the cameras and then E1, E2, E3 and E4 hid behind an obstacle to avoid being a source of distraction for the dog (Fig.1d). The owner went to the starting point of the straight-line walk, facing Camera 1, called the dog and launched the web application. As for dogs tested with the five-person group, the 10-second preparation phase then began, and when the sound signal was emitted at the end of the countdown, the owner turned 180 degrees and started walking in the first speed condition (see Fig.1e). The owner changed speed at each sound signal, which was emitted every 15 seconds. The owner wore headphones and could communicate with the dog during the preparation phase but not during the straight-line walk.

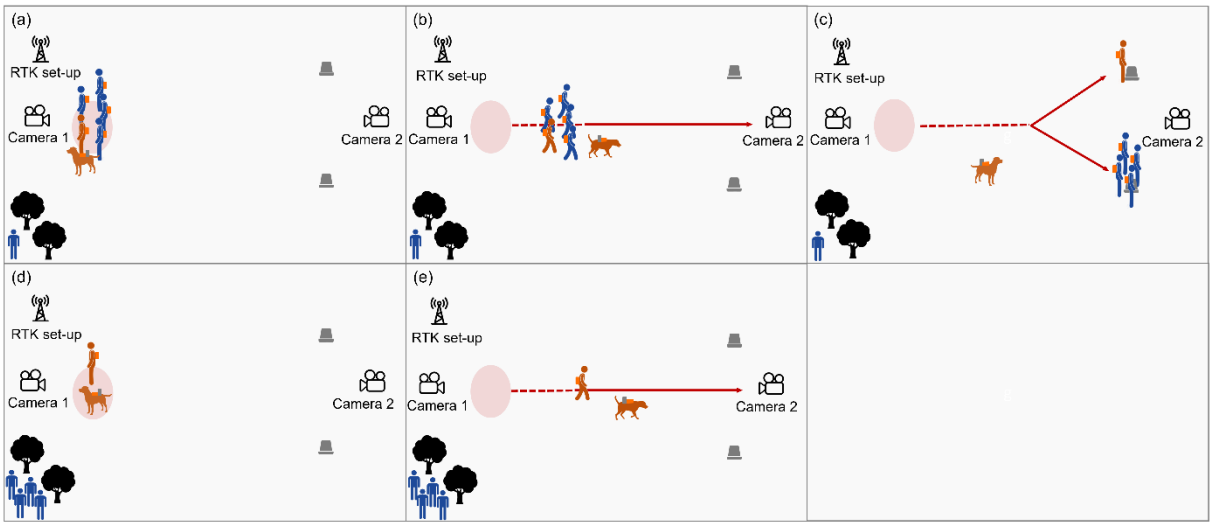


Figure1. Experimental procedure. GPS devices are represented by orange boxes on the

266 humans' and dogs' backs. A GoPro© camera was attached to the dog's harness. The owner is
267 represented in brown. Pink circles represent the starting point of the straight-line walk.

268

269 - Group separation for dogs with their owner and four other people (n = 20)

270 For the dogs tested with the five-person group, the group split up at the end of the 45-second
271 walk: the owner walked towards a 20 cm high post, while the other members of the group (the
272 accompanying person, E1, E2 and E3) walked to the other 20 cm high post (Fig.1c). The
273 humans then stayed still for 1 min. The posts were 10 m apart and 60 m away from the starting
274 point of the straight-line walk. The owners were randomly assigned one side of the post to walk
275 to, and the posts were counterbalanced.

276

277 *Data analysis*

278 - Straight-line walk with the owner alone (n = 20) vs with the owner and four other people
279 (n = 20)

280 We first checked that the people followed the protocol of the straight-line walk. To verify that
281 the humans walked faster in the fast walk condition compared to the slow walk condition, we
282 ran a linear mixed effects model (LMM) in R (version 4.4.1; https://www.R-project.org) by
283 using the 'glmmTMB' package, with a gaussian error distribution. The owner's speed was the
284 dependent variable, and we included walking speed condition (2 levels: slow walk, fast walk),
285 experimental group (2 levels: owner alone and owner and four other people) and the interaction
286 between these factors as fixed effects. For dogs observed with the five-person group, we also
287 modeled the surface area taken up by the five humans by using the 'glmmTMB' package with
288 a gaussian error distribution. We included the period of the walk (3 levels: the first 15 seconds

289 of the walk, the next 15 seconds, and the last 15 seconds) as fixed effects. We included dog ID
290 as random effects in both models, and an as the position data were computed every 0.25
291 seconds, each data point was very dependent on the previous one, so we included an
292 autocorrelation structure of order 1 (AR1).

293 Variables analysed for the straight-line walk were taken from Lamontagne et al. (2023) study.
294 The definitions of the variables are provided in Table 1. A blind coder recorded temporal
295 synchronization and dog gazing behaviour data by visual inspection of the video recordings
296 using Media Player Classic Home Cinema software (version 1.7.13, https://mpc-hc.org). A
297 second blind coder independently coded a randomly selected subset of 45% of the data. We
298 assessed the inter-rater reliability using Pearson's correlation and found a high level of
299 agreement between raters (latency: $R^2 = 0.93$, $P < 0.001$; gaze behaviour: $R^2 = 0.96$, $P < 0.001$).
300 We ran a Generalized Linear Mixed Model (GLMM) to model the distance between the dog
301 and the owner (location synchronization), using the 'glmmTMB' package, with a gamma
302 distribution for errors and log link function. The difference between the dog's speed and the
303 model speed (activity synchronization) was modeled with a GLMM using the 'glmmTMB'
304 package with a zigamma distribution for errors and log link function. In both models, we
305 included experimental group (2 levels: owner alone and owner and four other people), speed
306 condition (3 levels: static, slow walk, fast walk) and the interaction between these factors as
307 fixed effects, dog sex and age as control variables, dog ID as random effects and an AR1.
308 The latency (temporal synchronization) was modeled with a proportional hazard regression
309 model using the 'coxme' package, with experimental group as predictor, dog sex and age as
310 control variables, and dog ID as random effects. We used video recordings and speed over time
311 graphs obtained from GPS data to determine when, if ever, the dogs changed their speed after
312 the humans' change of speed. Latencies were identified by detecting a change in the dogs' gait

313 on the video recordings and a corresponding change in slope in the speed curves. Four gaits
314 were considered: stillness, walk, trot and gallop.
315 The time spent gazing at the owner was analysed with a LMM using the 'lme4' package. We
316 included experimental group, speed condition and the interaction between these variables as
317 fixed effects, dog ID as random effects and the dog's sex and age as control variables.
318

319 **Table 1.** Definitions of the dependent variables studied for the straight-line walk.

	Dependent variable	**Definition**
Location synchronization	Distance between the dog and the owner	Distance in metres between the dog and the owner, 180 values per dog, calculated every 0.25 seconds from GPS data.
Activity synchronization	Difference between the dog's speed and the owner's speed	Difference in absolute value between the dog's raw speed in metres per second and the owner's raw speed in metres per second, 180 values per dog, calculated every 0.25 seconds from GPS data.
Temporal synchronization	Latency	Time delay in seconds for the dog to change its speed after the owner changed speed, maximum two values per dog, calculated from video recordings and GPS data.
Gazing behaviour	Time spent gazing at the owner	Time in seconds the dog spent with its nose oriented towards the owner, three

	values per dog, calculated from video recordings.

320

321 - Group separation for dogs with their owner and four other people (n = 20)

322 During the separation phase (Fig.1c), we measured the distance between the dog and the owner
323 from GPS data, as well as the distance between the dog and the accompanying person who
324 remained within the group. Based on these distances, we recorded the first person whom the
325 dog followed (Table 2). The first person followed was the one whose distance to the dog either
326 decreased or remained constant, while the distance between the dog and the other person
327 increased. None of the dogs moved away from both the group and their owner, they all moved
328 in a direction that brought them closer to one of the humans. We conducted a chi-square test
329 with the function 'chisq.test' to compare the number of dogs who first followed their owner to
330 the number of dogs who first followed the accompanying person, and the group by extension.
331 We also conducted chi-square tests to compare the number of dogs who followed the person
332 (owner or accompanying person) they were closest to just before the group split to those that
333 did not, and the number of dogs who went to the left side to those who went to the right side,
334 regardless the side where the owner went.

335 We analysed the length of time that the dog spent following the person or people (Table 2) with
336 an anova, using the 'aov' function, including the first person followed by the dog (two levels:
337 owner or accompanying person, i.e. the group) as an independent variable and the dog's sex and
338 age as control variables.

339 As for the straight-line walk, the blind coder recorded dog gazing behaviour data using video
340 recordings, and we a high level of agreement between raters (R^2 = 0.99, P < 0.001). The dog's
341 gazing behaviour was analysed with an LMM, using the 'lme4' package, with the person gazed

342 at (two levels: owner or accompanying person) as a fixed effect, dog's sex and age as control
343 variables and dog ID as random effects.

344 Model assumptions were graphically checked using the 'DHARMa' package, and the
345 'survminer' package for the model of latency (see Residuals diagnostic plots in the
346 Supplemental File 1). For all models, we assessed whether the full model significantly differed
347 from the corresponding null model (which included only control variables and random factors)
348 via Likelihood Ratio Test, using the 'anova' function with the 'chisq' argument. If the null-full
349 model comparison was significant, we reported the estimates and standard errors (SE) for the
350 variables, obtained using the 'summary' function. We also reported 95% confidence intervals
351 (95% CI), obtained using the 'confint*'* function with the 'profile' argument. Test statistics (from
352 Wald chi-square tests) were calculated using the 'Anova' function from the 'car' package with
353 Type 3 sum of squares. Where needed, we performed post-hoc comparisons by using the
354 'emmeans' package with the Kenward-Roger approximation and Tukey corrections for
355 multiple testing.

356

357 **Table 2.** Definitions of the dependent variables studied for the group separation phase.

Dependent variable	Definition
First person followed	Person (owner or accompanying person, i.e. the group) who the dog followed after the group separated, as indicated by GPS data.
Time the dog spent following the person	Time during which the distance between the dog and the first person the dog followed did not increase, from GPS data.

Gazing behaviour	Time in seconds the dog spent with its nose oriented towards the person, two values per dog (one for gaze behaviour towards the owner and one for gaze behaviour towards the accompanying person), calculated from video recordings.

RESULTS

Control of compliance with the straight-line walk protocol

The owners followed the speed condition instructions, as there was a significant difference between the full- and the null-model ($\chi^2_3 = 62.97$, $P < 0.001$). The owner's walking speed significantly differed as a function of walking speed condition, with no difference between owners alone and owners with four other people (Table 3). The owners walked faster in the fast walk condition (mean ± SE = 1.50 ± 0.01 m / s) compared to the slow walk condition (mean ± SE = 0.91 ± 0.01 m / s). For information, when owners were in the static condition, thus not walking, their speed was 0.11 ± 0.01 m / s.

For dogs tested with their owner and four other people, the five humans maintained their group configuration throughout the test, as we found no significant difference between the full and the null model of the surface area taken up by the group ($\chi^2_2 = 3.85$, $P = 0.146$).

Table 3. Results of the GLMM of the owner's speed.

Fixed effect	**Estimate**	**SE**	**z value**	**95% CI**	χ^2	***P***
Intercept	0.92	0.07	14.08	[0.78;1.05]	198.20	<0.001

Experimental group (owner and four people)	-0.01	0.09	-0.13	[-0.20;0.17]	0.02	0.894
Speed condition (fast walk)	0.21	0.03	6.16	[0.15;0.28]	37.90	<0.001
Experimental group (owner and four people): speed condition (slow walk)	-0.04	0.05	-0.74	[-0.12;0.06]	0.55	0.459

The predictors were dummy coded, with experimental group (owner alone) and speed condition (slow walk) being the reference categories. Estimate ± SE refers to the difference of the response between the reported level of this categorical predictor and the reference category of the same predictor.

Straight-line walk with the owner alone (n= 20) vs with the owner and four other people (n = 20)

- Location synchronization

To study location synchronization, we analysed the distance between the dog and the owner. The full model was not significantly different from the null model ($\chi^2_5 = 3.57$, $P = 0.612$). The dogs stayed at a distance of 4.93 ± 0.07 m from their owner during the walk.

- Activity synchronization

Regarding the difference between the dog's speed and the owner's speed, we found a significant difference between the full- and the null-model ($\chi^2_5 = 37.26$, $P < 0.001$). There was a significant interaction between experimental group and speed condition (Table 4). Post-hoc tests showed

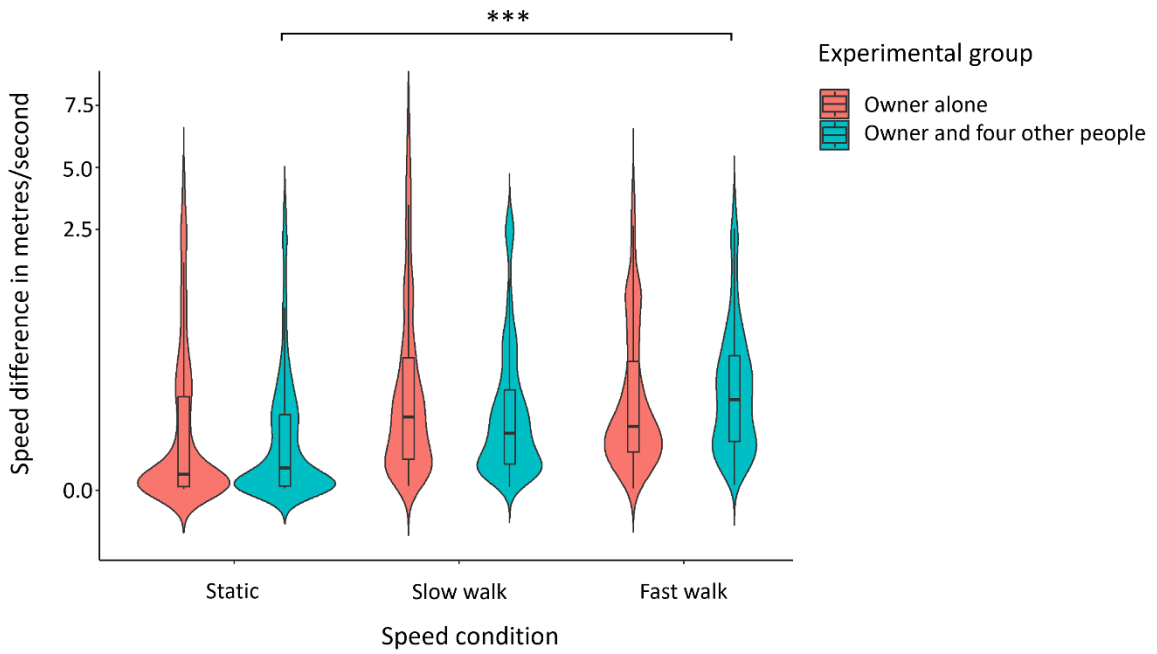
a significant difference for dogs with their owner and four other people (Fig.2), with a larger speed difference when the humans were walking fast compared to when they were walking slowly (ratio ± SE = 0.47 ± 0.06, z ratio = -5.72, $P < 0.001$, Cohen's d = -1.52). All other pairwise comparisons did not reveal any significant differences (Table S2 in Supplemental file 1). For information, dogs had a speed of 0.52 ± 0.02 m / s when the humans were static, 1.40 ± 0.03 m / s when the human were walking slowly and 1.74 ± 0.02 m / s when the humans were walking fast.

Table 4. Results of the GLMM of the difference between the dog's speed and the owner's speed.

Fixed effect	**Estimate**	**SE**	**z value**	**95% CI**	χ^2	***P***
Intercept	-1.14	0.26	-4.46	[-1.65;-0.63]	19.84	<0.001
Experimental group (owner and four people)	-0.19	0.21	-0.88	[-0.61;0.23]	0.77	0.381
Speed condition (slow walk)	0.23	0.14	1.68	[-0.04;0.50]	5.90	0.052
Speed condition (fast walk)	0.31	0.13	2.38	[0.05;0.56]		
Dog age	-0.02	0.04	-0.50	[-0.10;0.06]	0.25	0.616
Dog sex (male)	0.14	0.19	0.75	[-0.22;0.50]	0.56	0.454
Experimental group (owner and four people): speed condition (slow walk)	0.20	0.19	1.06	[-0.17;0.58]	5.95	0.050
Experimental group (owner and four people): speed condition (fast walk)	0.44	0.18	2.43	[0.09;0.80]		

The predictors were dummy coded, with experimental group (owner alone) speed condition (static), and dog sex (female) being the reference categories. Estimate ± SE refers to the

402 difference of the response between the reported level of this categorical predictor and the
403 reference category of the same predictor.



404

405 **Figure2.** Effect of speed condition on speed difference for dogs with their owner and four
406 people during the straight-line walk. Data exceeding 2.5 m / s were squashed. *** $P \leq 0.001$

407

408 - Temporal synchronization

409 To study temporal synchronization, we analysed the dog's latency to change speed when the
410 owner changed speed. All dogs exhibited temporal adjustment during the change of speed
411 condition. The change in dog's speed was in accordance with the owner's change in speed: dogs
412 accelerated when humans increased their speed (static to slow walk, static to fast walk, slow
413 walk to fast walk) and slowed down when humans decreased their speed (slow walk to static,
414 fast walk to static, fast walk to slow walk). The null-full model comparison was not statistically
415 significant ($\chi^2_1 = 0.02$, $P = 0.886$). Dogs adapted their speed in 2.19 ± 0.18 s.

416 - Gazing behaviour

To analyse dogs' gazing behaviour towards their owner, we measured the time the dog spent gazing at the owner. The full model differed from the null model (χ^2_5 = 11.94, P = 0.036).

There was an effect of speed condition on the time the dog spent gazing at their owner (Table 5, post-hoc tests: static – slow walk: estimate ± SE = -0.96 ± 0.58, t_{75} = -1.64, P = 0.234, Cohen's d = -0.38; static – fast walk: estimate ± SE = -1.70 ± 0.58, t_{75} =- 2.92, P = 0.013, Cohen's d = -0.68; slow walk – fast walk: estimate ± SE = -0.74 ± 0.58, t_{75} = -1.27, P = 0.415, Cohen's d = -0.30). Dogs spent more time gazing at their owner in the fast-walk condition compared to the static condition (Fig.3).

Table 5. Results of the LMM of the time spent gazing at the owner.

Fixed effect	**Estimate**	**SE**	**t value**	**95% CI**	χ^2	***P***
Intercept	2.43	0.78	3.13	[0.95;3.92]	9.81	0.002
Experimental group (owner and four people)	-0.91	0.82	-1.11	[-2.49;0.66]	3.08	0.079
Speed condition (slow walk)	0.82	0.82	1.00	[-0.75;2.39]	8.55	0.014
Speed condition (fast walk)	1.72	0.82	2.09	[0.15;3.29]		
Dog age	0.07	0.11	0.68	[-0.13;0.27]	0.46	0.497
Dog sex (male)	0.38	0.48	0.79	[-0.53;1.30]	0.63	0.428
Experimental group (owner and four people): speed condition (slow walk)	0.27	1.16	0.23	[-1.95;2.49]	0.09	0.957
Experimental group (owner and four people): speed condition (fast walk)	-0.05	1.16	-0.04	[-2.27;2.17]		

The predictors were dummy coded, with experimental group (owner alone) speed condition (static), and dog sex (female) being the reference categories. Estimate ± SE refers to the difference of the response between the reported level of this categorical predictor and the reference category of the same predictor.

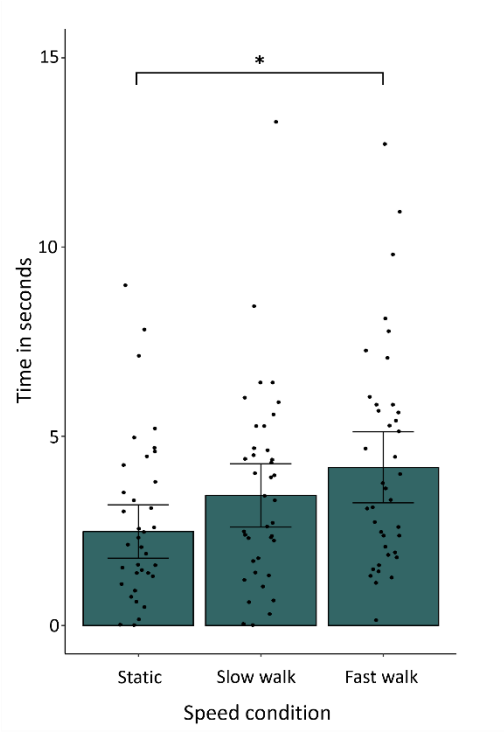


Figure3. Effect of speed condition on the time spent gazing at the owner during the straight-line walk. Data are presented as mean ± SE, dots represent data points. * $0.01 < P \leq 0.05$

Group separation for dogs with their owner and four other people (n = 20)

- First person followed

For the group of dogs tested with their owner and four other people, the group of five humans separated at the end of the straight-line walk, with the owner going to one post and the rest of the group going to another. When the group separated, all dogs either followed their owner or the accompanying person, i.e. the group by extension. Significantly more dogs first followed

the accompanying person, and thus the group (n = 15) than the owner (n = 5) (Fig.4a, χ^2_1 = 5.0, P = 0.025, Cohen's h = 1.05). The number of dogs who followed the person they were closest to just before the group separated (n = 11) was not significantly different from the number of dogs who did not follow the person they were closest to just before the separation (n = 9) (χ^2_1 = 0.2, P = 0.655). There was no side bias (χ^2_1 = 0.8, P = 0.371), 8 dogs went to the right side, 12 dogs went to the left side.

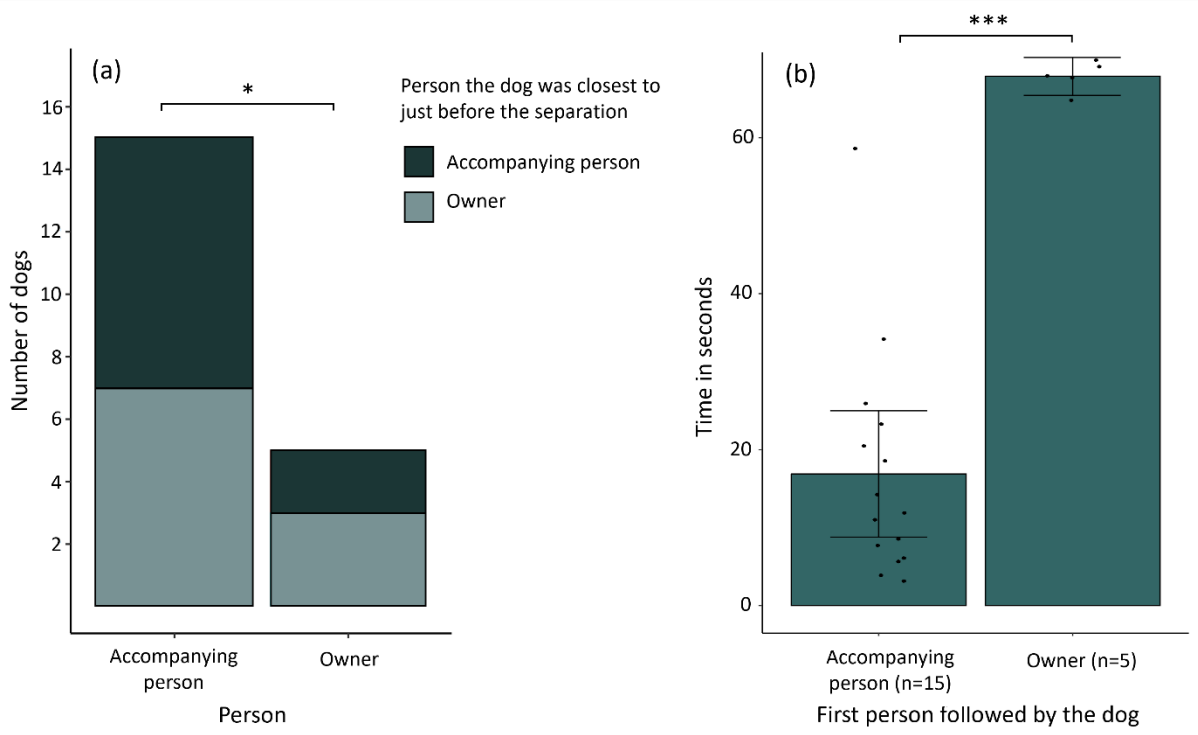


Figure4. Number of dogs that first followed the owner or group during group separation (a) and time the dog spent following the person or people (b). Data are presented as mean ± SE, dots represent individual data points. * $0.01 < P \leq 0.05$, *** $P \leq 0.001$

- Time the dog spent following the person

The length of time the dog spent following the person differed depending on the person the dog followed first ($F_{1,16}$ = 58.70, P < 0.001, η^2 = 0.52) with no main effect of dog age ($F_{1,16}$ = 0.02,

454 P = 0.885) and sex ($F_{1,16}$ = 1.62, P = 0.221). The dogs spent longer with the first person they
455 followed when this person was their owner than when the person was the accompanying person,
456 and thus the group (Fig.4b). Dogs that first followed their owner stayed close to their owner
457 until the end of the experiment. Among the 15 dogs that first followed the group, 1 dog remained
458 with the group until the end of the experiment, and 14 went back to their owners before the end
459 of the experiment. Among these 14 dogs, 7 went back to their owner while the humans were
460 walking towards the posts, and 7 went back to their owner when the humans were standing still
461 at the posts.

462 - Gazing behaviour

463 The null-full model comparison was not significant (χ^2_1 = 0.37, P = 0.541), indicating that dogs
464 gazed equally at the owner and the accompanying person. The dogs spent 8.49 ± 1.10 s gazing
465 at their owner and 9.43 ± 1.44 s gazing at the accompanying person within the group.

466

467 **DISCUSSION**

468 We investigated the effect of the number of human agents and owner's presence on dogs'
469 behavioural synchronization to their owners. Our protocol consisted of two phases: first, for the
470 straight-line walk, we used the same protocol as Lamontagne et al. (2023), but with a larger
471 group size. Second, the group separation phase was inspired by Nagasawa et al. (2020) study.
472 We expected that during the straight-line walk, the dogs would exhibit a higher degree of
473 locomotor synchronization to that of their owners, and increased gazing behaviour towards their
474 owner when with their owner and four other people than for dogs with their owner alone.
475 Additionally, for dogs who were with the five-person group, we expected that the dogs would
476 follow their owner – the person with the highest social value – over the group of four humans.

The predictions were not reflected in our results. Our findings for the straight-line walk show no significant difference between the two experimental groups for the three components of behavioural synchronization and gaze behaviour. For the group separation phase, contrary to our prediction, most of the dogs went to the group first.

Our results on the straight-line walk do not follow our predictions but are consistent with those of Lamontagne et al. (2023). Both studies concur that during the straight-line walk, regardless of the number of humans present, the dogs stayed at a distance of about 5 m from their owner (location synchronization), maintained a speed difference of less than 1 m/s compared to the owners' speed (activity synchronization) and took just over 2 seconds to adjust their speed after the owners' change in speed (temporal synchronization). As for the dog's gazing behaviour, we did not find an effect of number of people on the dog's visual attention, contrary to the previous study. Lamontagne et al. (2023) involved only working dogs, selected to be attentive to humans (Wobber et al., 2009); in the current study, we accepted all breeds. It is therefore possible that the group effect on dogs' visual attention is only present for working breeds, selected for this purpose, and does not emerge when a wider variety of breeds of domestic dog are represented.

Regarding the separation phase, we found that out of 20 dogs, 15 followed the rest of the group and not their owner. It is unlikely that dogs followed the rest of the group because they initially paid no attention to their owner during the separation phase, as half of the dogs were right next to their owner when the latter moved away from the group, and they spent as much time gazing at their owner as at the rest of the group. The dogs initially followed the group, but we did find an effect of affiliation, as 14 out of 15 dogs subsequently went back to their owners afterwards. Our results indicate that dogs tended to follow the group rather than their owner, and that affiliation influenced this tendency with a delayed effect. We thus found an effect of level of familiarity, similar to the findings Nagasawa et al. (2020), but it manifests differently, likely because our studies were conducted in different contexts. Nagasawa et al. (2020) showed that

dogs were less likely to go to larger groups if familiar people were in the smaller groups. However, in their study, dogs had to wait 3 seconds before moving towards the humans, and the humans gave a verbal cue, "it looks good," while standing near a container with food. In contrast, in our protocol, the humans gave no verbal cues, and the dogs could move even at the start of the group separation, as our intent was to observe whom the dogs would follow in the absence of food rewards and communication signals from humans. Furthermore, in Nagasawa et al. (2020) study, the dogs had been trained to receive food by following humans, and the familiar people spent 10 minutes interacting with and feeding the dogs. These previous interactions were likely responsible for the dogs' tendency to go to familiar people. We expand on the results of the influence of familiarity on dogs' behaviours, by showing that affiliation with the owner has a delayed influence on dogs' group-following behaviour.

Our findings did not allow us to conclude that there was a significant group effect during the straight-line walk. However, we did find a group effect at the beginning of the separation phase. At first glance, these results may seem contradictory. Why, then, was the group effect not apparent during the straight-line walk? This could be due to a genuine lack of difference, meaning the number of people have no effect on dogs' locomotor synchronization with humans, or a lack of statistical power due to variability in our dataset, or due to our measurements which may have not captured the impact of number of people on dogs' synchronization. It is unlikely that the number of people is not a social modulator of dogs' behavioural alignment with humans, given that most of the dogs followed the group rather than their owner during the separation phase, and that previous studies have shown an effect of number of humans on dogs' behavioural response (Nagasawa et al. 2020; Kubynyi et al. 2003b; Kundey et al. 2012). It is possible that dogs' locomotor synchronization was already at its maximum level due to the presence of the owner, leaving no room for enhancement with an additional social modulator. This is supported by the fact that we observed the same level of dogs' locomotor

synchronization whether the owner was alone, with two other people or with four other people in the current and previous studies (Lamontagne et al., 2023). It also aligns with the literature showing that owners are dogs' preferred social partners and their presence significantly influences dogs' behavioural responses (Feuerbacher & Wynne, 2014, 2017; Horn et al., 2013). However, most of the dogs did not immediately go to their owner when the group separated, their first response was to follow the group. This suggest that the effects of affiliation and number of people on dogs' following behaviour are based on different cognitive processes, with the effect of group size producing a faster behavioural response in dogs which is then overrided by the effect of affiliation. This study does not allow to test the cognitive processes involved, but we can speculate about a few possibilities. One is that dogs' group-following behaviour may rely on mirror neurons, which are known to underpin imitative behaviour in humans and other mammals, though they have not yet been studied in dogs (Bonini et al., 2022). Mirror neuron activation increases with group size in humans (Cracco & Brass, 2018a,b,c; Cracco et al., 2015, 2016, 2019), so a similar mechanism in dogs might explain their initial group-following behaviour, which was later overridden by the effect of affiliation. Another possibility is that the owner and the four humans provided conflicting information about the walking direction when the group split. The dogs may have followed the four humans because they were a larger source of information, aligning with the results of Kundey et al. (2012); they then went back to their owner when the latter was too far away for too long, as dogs typically do during walks (Foltin & Ganslosser, 2021). Lastly, owners are social attractors for dogs, but they are not the only ones (Cook et al., 2016; Feuerbacher & Wynne, 2017). The interactions with the humans at the beginning of the procedure may have made them attractive to the dogs. The four humans may have temporarily offered a stronger attraction than the owner alone, leading the dogs to follow them before going back to their owner. Our study thus provides insights for

551 further research into the mechanisms underlying dogs' behavioural alignment with groups of
552 humans.

553 While the presence of the owner provided valuable information on the effect of affiliation on
554 dogs' behaviours, it also constitutes a limitation in our study. To mitigate the affiliation effect,
555 it would be valuable to replicate the protocol by substituting the owner with a familiar person.
556 If dogs' synchronization with humans indeed relies on motor resonance, this would result in
557 dogs synchronizing more with humans in a group compared to a single human. Another
558 limitation of our study is that we conducted the experiment in an entirely open environment
559 which necessitated the selection of dogs with a minimum level of recall training for safety
560 reasons. In addition, the GPS equipment prevented the inclusion of dogs weighing less than 7
561 kg in our sample. Although our sample encompasses various breed types, our inclusion criteria
562 somewhat restricted the representativeness of the overall canine population. Finally, we
563 instructed participants to refrain from looking at or communicating with the dog during the
564 walk, nor to engage in conversation with each other. We acknowledge that this approach may
565 not fully replicate naturalistic conditions where dogs and humans typically look at each other
566 during walks, but we implemented this rule to attribute the dogs' behaviours solely to the
567 humans' locomotor behaviours.

568

569 **Conclusion**

570 In this study, we investigated dogs' locomotor synchronization with their owner alone or
571 accompanied by four other people. As in the study conducted by Lamontagne et al. (2023), we
572 found no significant effect of the number of human agents on dogs' behavioural
573 synchronization. However, dogs followed the largest stimulus (i.e. the four humans) when the
574 group split into two, but this behaviour was transient, due to the attracting effect of the owners.

Our study advances our comprehension of the social modulation of dogs' behavioural alignment with humans and also lays the groundwork for future behavioural and neurological studies aimed at elucidating its underlying neurocognitive processes.

Data Availability statement: Datasets are accessible in the Open Science Framework repository at the following link:

https://osf.io/fts7w/?view_only=0ad51602f84c455fae716b27c2caa697

Conflict of interest: The authors have no relevant conflict of interest to disclose.

Acknowledgements: The authors are grateful to the owners and their friends and relatives who volunteered for the study. The authors also thank Maëlle Delbos, Thomas Bouvier and Mathilde Chevalier for their roles as E1, E2, and E3, and Marine Brunel for coding the video recordings.

Funding: This work was supported by the National Association for Research and Technology (ANRT), the association *Agir pour la Vie Animale*, the French National Centre for Scientific Research (CNRS), and Aix-Marseille University.

Author contributions:

Angélique Lamontagne: conceptualization, methodology, formal analysis, investigation, data curation, writing original draft, visualization. Thierry Legou: conceptualization, methodology, validation, investigation, writing review and editing. Thierry Bedossa: conceptualization, resources, funding acquisition. Florence Gaunet: conceptualization, methodology, validation, writing review and editing, supervision.

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Title: Social Modulation of Dogs' Behavioural Synchronization with Humans: Effect of Number of People and Owner's Presence

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Table S1. List of breeds in each experimental group

Prior to the procedure, the dogs were randomly assigned to one of the two experimental groups, by counterbalancing sexes and with no consideration of the dogs' breeds.

Owner alone (*n* = 20)	**Owner with four other people (*n* = 20)**
1 Australian Shepherd	1 Australian Shepherd
1 Belgian Shepherd	1 Beauceron
1 Border Collie	4 Belgian Shepherd
1 Cocker Spaniel	1 Border Collie
1 German Shepherd	1 Alaskan Malamute
1 Golden Retriever	1 German Shepherd
1 Husky	1 Labrador Retriever
1 Miniature American Shepherd	4 Mixed
6 Mixed	1 Mixed Border Collie
1 Mixed American Staffordshire Terrier	1 Mixed Husky
2 Staffordshire Bull Terrier	3 Mixed Shepherd
3 White Swiss Shepherd Dog	1 Mixed Scenthound

Table S2. Post-hoc tests for the interaction between speed condition and experimental group on the activity synchronization variable.

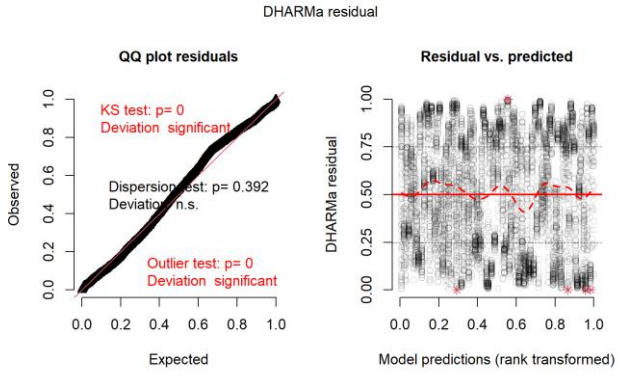
Post-hoc comparison	Ratio	SE	z ratio	*P*
Owner alone static – Owner and four people static	1.21	0.26	0.88	0.953
Owner alone static – Owner alone slow walk	0.79	0.11	-1.68	0.544
Owner alone static – Owner and four people slow walk	0.78	0.17	-1.15	0.860
Owner alone static – Owner alone fast walk	0.74	0.10	-2.38	0.164
Owner alone static – Owner and four people fast walk	0.57	0.12	-2.63	0.091
Owner and four people static – Owner alone slow walk	0.66	0.14	-1.95	0.375
Owner and four people static – Owner and four people slow walk	0.65	0.09	-3.21	0.068
Owner and four people static – Owner alone fast walk	0.61	0.13	-2.31	0.189
Owner and four people static – Owner and four people fast walk	0.47	0.06	-5.72	<0.001
Owner alone slow walk – Owner and four people slow walk	0.99	0.21	-0.07	1.000
Owner alone slow walk – Owner alone fast walk	0.93	0.12	-0.59	0.992
Owner alone slow walk – Owner and four people fast walk	0.72	0.15	-1.55	0.632
Owner and four people slow walk – Owner alone fast walk	0.94	0.20	-0.28	0.999

Owner and four people slow walk – Owner and four people fast walk	0.73	0.09	-2.46	0.137
Owner and four people fast walk – Owner and four people fast walk	0.77	0.17	-1.20	0.837

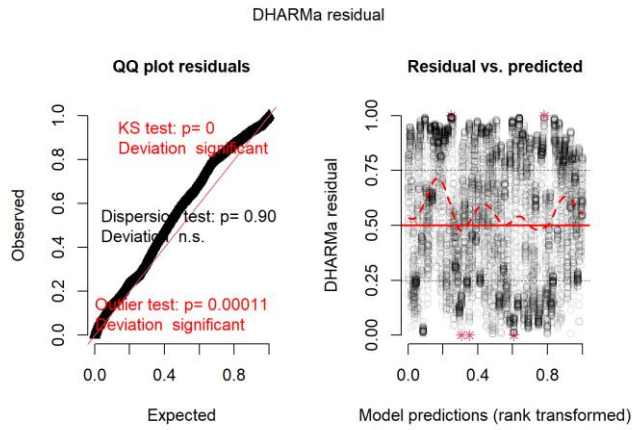
Residuals diagnostic plots – obtained using the DHARMa package

Note: KS test and outlier test were sometimes significant, it was likely due to the large amount of values, which makes these tests very sensitive to the slightest deviation from uniformity.

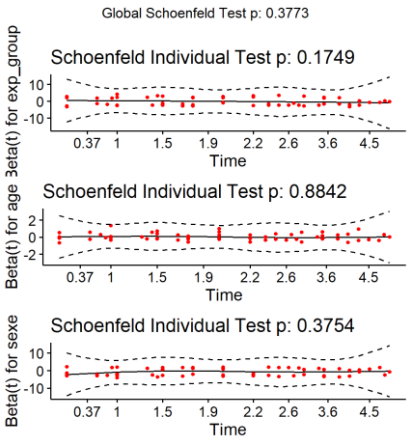
Model of distance:



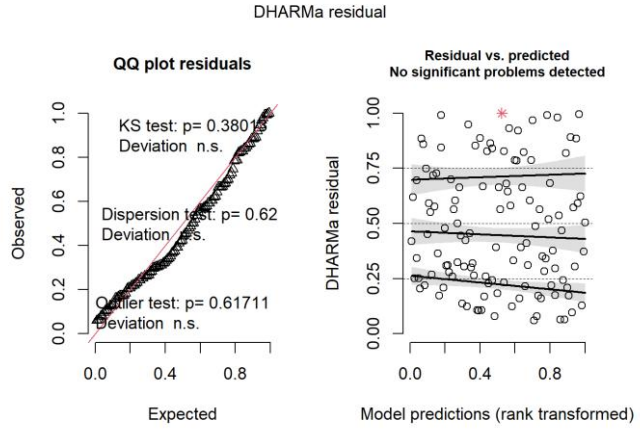
Model of speed difference:



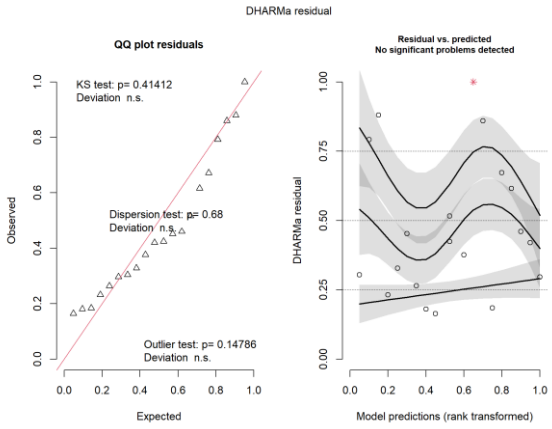
Model of latency (obtained with the *ggcoxzph* function from the *survminer* package)



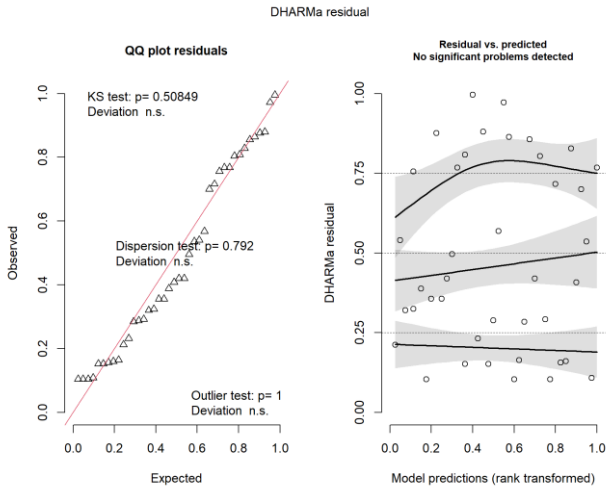
Model of time spent gazing during the straight-line walk:



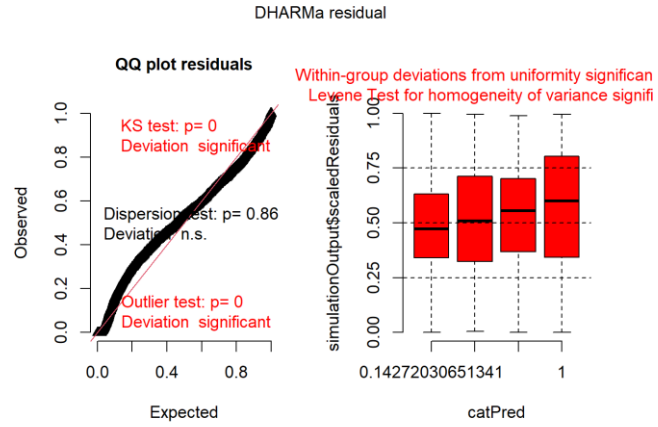
Model of time spent following during the group separation phase:



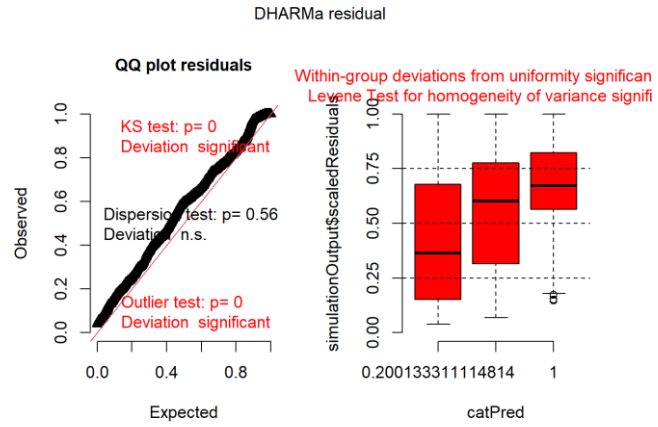
Model of time spent gazing during the group separation phase:



Model of owners' speed during the straight-line walk:



Model of the surface area taken up by the five humans:



4. Modulation de la synchronisation comportementale chez le chien par le type d'agent social

Les chiens, en tant qu'espèce sociale, se synchronisent spontanément avec leurs congénères (Duranton, 2020). La domestication et l'exposition à l'humain dès les premiers jours de vie des chiens ont mené à l'émergence de capacités cognitives habituellement observées au niveau intraspécifique. Notamment, les chiens sont sensibles aux signaux sociaux humains et se synchronisent avec eux, en particulier leurs propriétaires (Duranton et al., 2017b; Heurlin et al., 2024, Lamontagne et al., 2023). Certaines études montrent même que les chiens utilisent aussi bien la démonstration humaine que celle d'un congénère pour accomplir une tâche et présentent davantage d'indicateurs comportementaux de réduction du stress, de recherche de proximité et d'exploration en présence de leur propriétaire qu'en présence d'un congénère vivant dans le même foyer (Fugazza et al., 2018b; Range & Virányi, 2013; Sipple et al., 2021). Comparer la cognition canine intraspécifique (entre chiens) et interspécifique (entre chiens et humains) permet ainsi de mieux comprendre à quel point l'enculturation humaine affecte les capacités sociales des chiens. Nous avons donc comparé la synchronisation locomotrice des chiens avec un congénère familier et avec un humain familier dans un environnement extérieur fermé, sans laisse. Notre hypothèse était que, du fait de schémas locomoteurs identiques, la synchronisation entre chiens serait plus prononcée que celle entre les chiens et l'humain. Nous nous attendions donc à ce que la distance (synchronisation de localisation) et l'écart de vitesse (synchronisation d'activité) soient plus faibles et que le temps passé avec les corps alignés (synchronisation d'activité) soit plus élevé en présence du congénère qu'en présence de l'humain. Nous avons également étudié la direction du regard des chiens et considérant que le regard est un mode de communication privilégié entre le chien et l'humain, nous avons supposé que les chiens porteraient une plus grande attention visuelle à l'humain familier qu'au congénère familier.

Nos analyses ont révélé que la distance était effectivement plus faible lorsque les chiens étaient avec le congénère familier, également que l'écart de vitesse était plus élevé avec l'humain, mais ce résultat ne concernait que les chiens qui ne vivent pas avec un congénère dans le foyer. Ces résultats soutiennent notre hypothèse, bien que l'effet observé sur l'écart de vitesse uniquement pour les chiens vivant sans congénère pose question quant à l'impact de l'expérience quotidienne sur la synchronisation locomotrice chez le chien. Il est raisonnable de considérer que les chiens vivant avec un congénère ont davantage d'expériences d'observations d'interactions interspécifiques par rapport à ceux qui ne cohabitent pas avec un chien. Il semble que ces expériences facilitent l'ajustement de la vitesse des chiens sur celle de l'humain. Cette étude nous amène ainsi à

réfléchir sur les mécanismes cognitifs sous-jacents à la synchronisation comportementale interspécifique, en particulier sur l'effet de l'expérience sur les représentations sensorimotrices de la marche chez le chien. Enfin, en ce qui concerne l'activité de regard, aucune différence significative n'a finalement été observée, contrairement à notre hypothèse. Cela suggère que l'attention visuelle marquée des chiens envers l'humain, démontrée dans la littérature, pourrait être spécifique aux propriétaires ou à certains contextes particuliers, dans des tâches de travail ou de problèmes insolubles par exemple, mais pas forcément lors d'interactions spontanées.

Article 5 : Lamontagne, A., Legou, T., Bedossa, T. & Gaunet. F. (in preparation). Temporary title: Familiar congener or familiar human: Who do pet dogs best synchronize with?

Familiar congener or familiar human: Who do pet dogs best synchronize with?

Data Availability statement: Datasets are accessible in the Open Science Framework repository at the following link:

https://osf.io/naxyp/?view_only=64d31c1f4ead417c958df9ebb6d26c86

Abstract:

Behavioural synchronization in dogs has been examined separately at intraspecific and interspecific levels. This study is the first to compare dogs' behavioural synchronization and gaze behaviour when with a familiar human (H) versus a familiar dog (D), while walking freely in an outdoor environment. Twenty pet dogs were observed under both experimental conditions. We hypothesized that dogs would demonstrate stronger location and activity synchronization with D than H due to similar locomotor patterns, while showing greater gaze attention towards H compared to D. Results revealed that the distance between dogs and D was significantly smaller than the distance between dogs and H, averaging 4 meters versus 6 meters. We also found a significant interaction between the type of agent and the presence of another dog in the household on speed adjustment: dogs exhibited a smaller speed difference with D (0.6 m/s on average) than with H (0.8 m/s on average), but only for dogs that did not cohabitate with another dog. No significant differences were observed in body alignment or gaze behaviour between the two experimental conditions. Overall, this study enhances our understanding of canine cognition in conspecific versus heterospecific contexts, and highlights how daily experiences, such as living with other dogs, influence dogs' ability to synchronize with individuals from different species.

Introduction:

Dogs, as social animals, are sensitive to the behaviours of their conspecifics and use this social information to communicate and adjust their own behaviours (Siniscalchi et al., 2018). Dogs are thus capable of synchronizing their behaviours with one another (Palagi & Cordoni, 2020), and this intraspecific synchronization depends on familiarity (Cimarelli et al., 2019). It has indeed been demonstrated that dogs synchronize more with familiar conspecifics than with unfamiliar ones, as evidenced by closer proximity between familiar dogs during off-leash walks (Duranton, 2020). Dogs have inherited their capacity for behavioural synchronization from their ancestors, wolves, which are known for their cooperative abilities in group activities such as breeding and hunting (Huber et al., 2014; Marshall-Pescini et al., 2017; Range & Virányi,

2014). This ability to synchronize behaviour with those of others is a key element in the social development of individuals and holds high adaptative value, as it is associated with increased survival, reduced energy expenditure, and greater social cohesion (Duranton & Gaunet, 2016a; Kavanagh & Winkielman, 2016).

Dogs, contrary to wolves, have the distinction of being a domesticated species. They were selected to assist and cooperate with humans in various tasks, such as guarding livestock and hunting. This led to the selection of specific traits in dogs, making them an intriguing model to study the evolution of social cognition (Range & Marshall-Pescini, 2022). Research over the past decades has revealed that dogs are sensitive not only to the behaviours of their conspecifics, but also to that of humans (Bensky et al., 2013; Huber et al., 2014; Kaminski & Nitzschner, 2013). Dogs exhibit social cognitive abilities towards humans that are typically seen at the intraspecific level, such as following ostensive and referential communication signals and synchronizing their behaviour with that of humans (Kaminski & Nitzschner, 2013). In recent years, there has been growing interest in the study of behavioural synchronization between dogs and humans (Duranton et al., 2017, 2018, 2019a; Heurlin et al., 2024; Lamontagne et al., 2023; Wanser et al., 2021). These studies have shown that when walking with humans, dogs stay close, adjust their speed to match that of the humans, and align their body orientation with that of humans. These abilities are present early in dogs, within the first few months of life (Duranton et al., 2022), depends on the level of familiarity (Duranton et al., 2019b; Duranton & Gaunet, 2016b) and are similar to those found in humans (Bray et al., 2021).

To the best of our knowledge, no studies have directly compared dogs' behavioural synchronization with conspecifics and with humans. The only comparative study available focuses on synchronization between dogs and humans versus between wolves and humans (Heurlin et al., 2024). The authors found that domestic dogs synchronize more with humans than socialized wolves or pack-living dogs. This aligns with a previous studies showing that dogs pay more attention to human behaviours than wolves do (Fugazza et al., 2023), and that wolves require extensive socialization to develop a comparable level of sensitivity to human actions (Virányi et al., 2008). Several studies have explored dogs' sensitivity to conspecifics versus humans, in other contexts than synchronized behaviours. One study showed that dogs are equally capable of learning socially from both a conspecific and a human during a problem-solving task (Fugazza et al., 2018) or in a local enhancement task (Range & Virányi, 2013). It has also been demonstrated that dogs living in the same household display stronger affiliative behaviours towards each other than towards their human caregiver (Cimarelli et al., 2019). However, dogs tend to show greater visual attention towards humans than towards conspecifics (Cimarelli et al., 2019; Range et al., 2009). Additionally, research has indicated that dogs behave differently when presented with a food reward in the presence of a conspecific or a

human, exhibiting more avoidance behaviours (staying at a distance or looking away, for example) when a conspecific is present than when a human is present (Pedretti et al., 2024).

Taken together, these findings suggest that while dogs possess similar social cognitive abilities towards humans and conspecifics (Cimarelli et al., 2019; Miklósi & Topál, 2013), their responses to intraspecific and interspecific cues may vary depending on the task or ability being tested. Dogs indeed appear to be respectively more sensitive to conspecifics with regards to affiliative behaviours and more attuned to humans with regards to referential communication. As for behavioural synchronization, it is difficult to draw conclusions because intraspecific and interspecific synchronization have been studied independently. This underscores the need for a direct comparison, which could provide valuable insights into dog cognition and the extinct to which humans' enculturation has impacted dogs' behaviours.

In this study, we addressed this gap by comparing the behavioural synchronization of 20 dogs between two experimental conditions: with a familiar conspecific and with a familiar human, during spontaneous movement in an enclosed outdoor space. We ensured that the level of familiarity with both the conspecific and the human was equal, as behavioural synchronization is known to depend on the level familiarity, and we aimed to prevent its effects from affecting our results. Based on the definition of Duranton and Gaunet (2016), we measured two components of behavioural synchronization: location synchronization (being in the same place at the same time) and activity synchronization (engaging in the same activity simultaneously). Our hypothesis was that it is easier to adjust to individuals with similar locomotor characteristics, so dogs would be more synchronized with the conspecific than with the human. Specifically, we expected dogs to have a smaller distance (location synchronization) and a smaller speed difference (activity synchronization), as well as more time spent with aligned body orientation (activity synchronization) when with the conspecific compared to the human. Additionally, we measured dogs' gaze behaviour and based on previous studies showing greater attention towards humans than towards conspecifics, we hypothesized that dogs would exhibit greater visual attention towards the familiar human, thus spending more time looking at the familiar human than at the familiar conspecific.

Material and method

Ethical note

This study was conducted in accordance with French regulations for animal welfare (Rural Code Article R214-17 and the official French Legal Code of Animals, 2018), the institutional guidelines of Aix-Marseille University, and the internal regulations of the dog club Agility du Gier, France, where the study was carried out. The study was exempt from ethical approval because it was conducted with privately owned pet dogs without any physical constraints nor

invasive samplings. All dog owners were recruited on a voluntary basis and signed an informed consent form. All the dogs were in good health, with no signs of aging or behavioural problems, based on information from the owners and observations by the experimenters. Data collection took place in March and April 2024 at the canine club, a familiar environment for the dogs who regularly attended sessions there. Each dog was given 5 to 10 minutes prior to the observations to get acquainted with the GPS equipment and was free to move within the testing area throughout the entire experimental procedure. The dog's owner always remained in the dog's sight, and we visually controlled for stress-associated behaviours.

Participants

The study included 20 adult dogs (10 males and 10 females) of various breeds or crossbreeds, aged between 1 and 8 years old (mean ± SD = 3.6 ± 2.3) and weighing a minimum of 7 kg (detailed information on the dogs' breeds and other demographic data is available in the dataset deposited in the OSF repository). Of the 20 dogs, 12 were the sole dog in their household, while 8 lived with one or more other dogs (6 with one other dog and 2 with three other dogs). All dogs were regular attendees of the canine club Agility du Gier, in classes such as education, dog dancing, or agility at a frequency of once a week to once a month. They were accustomed to walking off-leash and wearing a harness. Each dog was observed in two conditions, in a randomized order: with the familiar dog (D), a 7-year-old female Australian shepherd, member of the dog club, and with the familiar human (H), a 48-year-old male, who was a dog instructor in the dog club. Dogs' behavioural synchronization with humans is not affected by their level of obedience training (Lamontagne et al., 2023), but we controlled that no verbal commands, instructions or food rewards were provided during the observations to ensure that the dogs' behaviours towards H were not influenced by training expectations.

D and H lived in the same household, and were consistently present at the club once a week. They had been members of the club before the dogs joined it. Consequently, the dogs interacted with D and H at the same frequency, ranging from one to four times per month (mean ± SD = 2.5 ± 1.4 times per month) during canine recess or walks outside of classes. The dogs did not attend the classes of H, but those of a different dog instructor. None of the dogs had never exhibited fear or aggressive behaviours towards D and H. At the time of the experiment, the dogs had known them for (mean ± SD) 3 ± 2.2 years.

Experimental set up and apparatus

The dogs were observed individually in a 25m x 25m (625m²) enclosed park at the dog club (Figure 1.A). The owner and an experimenter (E1) were positioned in the center of the test area during the observations. For half of the dogs, E1 was on the owner's right (as illustrated in

Figure 1), for the other half, E1 was on the owner's left. Another experimenter (E2) remained outside the test area to monitor the experimental procedure. The presence within the test area of the owner and E1, who lived in the same household as D and H, was necessary, as pre-tests without their presence showed that dogs and the D stayed near the exit door of the test area and that dogs interacted poorly with D and H. This behaviour aligned with previous findings indicating that dogs exhibit more motionlessness and reduced interactions with other individuals in the absence of their owner compared to when their owner is present (Mariti et al., 2018; Palestrini et al., 2005; Prato-Previde et al., 2003).

The dogs, D and H wore harnesses to which a Global Positioning System (GPS) rover was attached (Figure 1.B). The GPS rovers were associated with a Real Time Kinematic (RTK) base station. The RTK base station provided real-time corrections to the GPS rovers, allowing for centimeter-level precision in positional data (see Lamontagne et al. 2023 for more details on the GPS rovers and RTK technology). Each rover recorded time, position, and the quality of the RTK correction every 0.25 seconds. The processing of GPS data resulted in four data points per second for the distance between the GPS rovers, and four data points per second for the speed of each GPS rover. Additionally, two cameras fixed on tripods filmed the test area from opposite angles, and a GoPro© camera was fixed on the harness worn by the dogs (Figure 1.B). E2 was positioned next to Camera 2 during the observations.

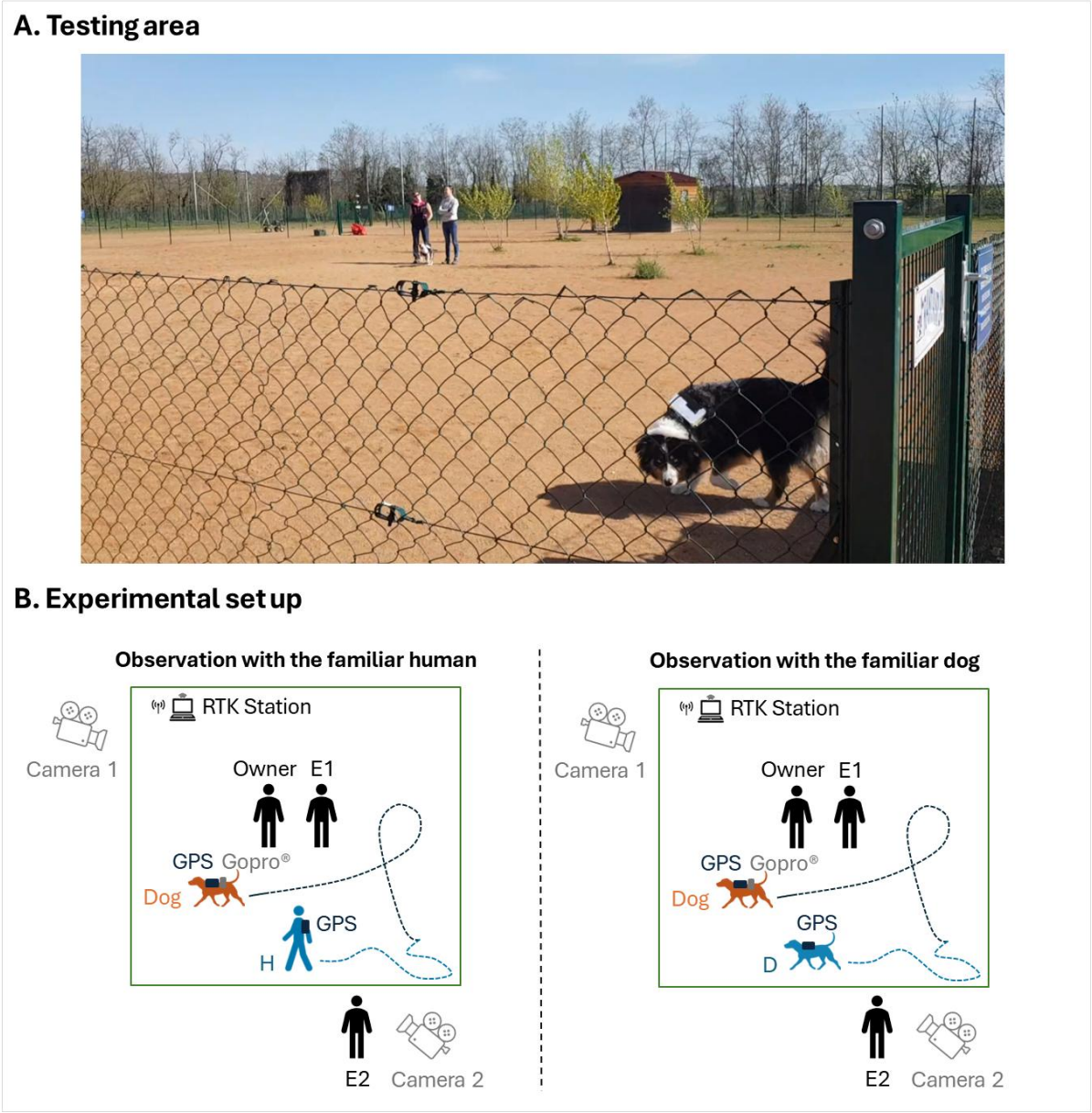


Figure 1. A. Testing area. In this example, the owner is on E1's right side, D is near the exit door and the dog is near E1 and the owner. B. Experimental set up for observations with D and H.

Experimental procedure

When the owner and their dog arrived at the test site, E1 assisted the owner in fitting the harness equipped with the GPS rover and the GoPro© camera onto the dog's back. E1 activated the GPS rover and the GoPro© camera, while E2 turned on Camera 1 and Camera 2 outside the test area. E1 and the owner positioned themselves side by side in the center of the park, remaining still, while the dog freely explored the area and became accustomed to the equipment for 5 to 10 minutes (Figure 2). The owner could communicate with their dog during the exploration phase. D and H were in a closed building during this time so the dog could not see them and they could not see the dog. E1 and the owner stopped looking at and talking to the

dog at the end of the exploration phase, and E2 brought the first agent (either D or H) to the entrance of the park, near Camera 2, while the second agent kept staying in the building. E2 activated the GPS rover on the agent's back and opened the fence so that the agent entered the park. E2 stayed still and silent outside the testing area, and monitored the timing of the observation through Camera 2's feed. The dog and the agent greeted each other, making eye contact and physical contact. The greeting phase was considered complete once the initial physical and eye contact ceased. The greeting phase with the first agent lasted (mean ± SD) 19.49 ± 8.48 seconds (with D (n=10) = 19.26 ± 10.50 seconds, with H (n=10) = 19.72 ± 6.41 seconds), based on visual inspection by E2 through Camera 2 and confirmed by video recordings checked by E1 and E2. The 5-minute observation began immediately after the greeting phase. We chose this duration based on pre-test results, which indicated that it was sufficient to capture the dogs' behaviours. E1, E2 and the owner remained still during this time. E2 signaled E1 and the owner to leave the test area with the dog and the agent at the end of the 5 minutes. Cameras and GPS rovers were turned off, and a 15-minute break followed, during which E1, E2 and the agent returned to the building, while the owner and their dog went for a short walk within the dog club premises. The dog did not wear the harness during the break. Observations were conducted on days without dog classes to ensure that no club members were present, and as the dog club was a private location, no other individuals besides the dog, the owner, E1, E2, D and H were present in the club, even during breaks. After the break, E1, E2, the owner, and the dog came back to the test area. The owner equipped again the dog with the harness, E1 activated the GPS rover and the GoPro© camera, while E2 turned on Camera 1 and Camera 2 outside the test area. E1 and the owner positioned themselves again in the center of the park and the dog was given 5 to 10 minutes to explore the area. E2 then brought the second agent to the entrance of the test area (Figure 2), activated the GPS rover on the agent's back, and opened the fence so that the agent entered the test area. The dog and the second agent greeted each other, the greeting phase lasted (mean ± SD) 20.38 ± 9.03 seconds (with D (*n*=10) = 23.61 ± 11.49 seconds, with H (*n*=10) = 17.14 ± 6.89 seconds), based on visual inspection by E2 through Camera 2 and confirmed by video recordings checked by E1 and E2. The 5-minute observation with the second agent started after the greeting phase. E2 monitored the timing and indicated to E1 and the owner to leave the test area with the dog and the agent at the end of the 5-minute observation. The dog remained off-leash, and no instructions were given to the dog during the entire experimental procedure. The participation lasted approximately one hour. Several dogs could be tested on the same day, but we do not believe the test with one dog affected subsequent tests with other dogs due to the general abundance of canine scents at the dog club and the familiarity of all participating dogs with these scents.

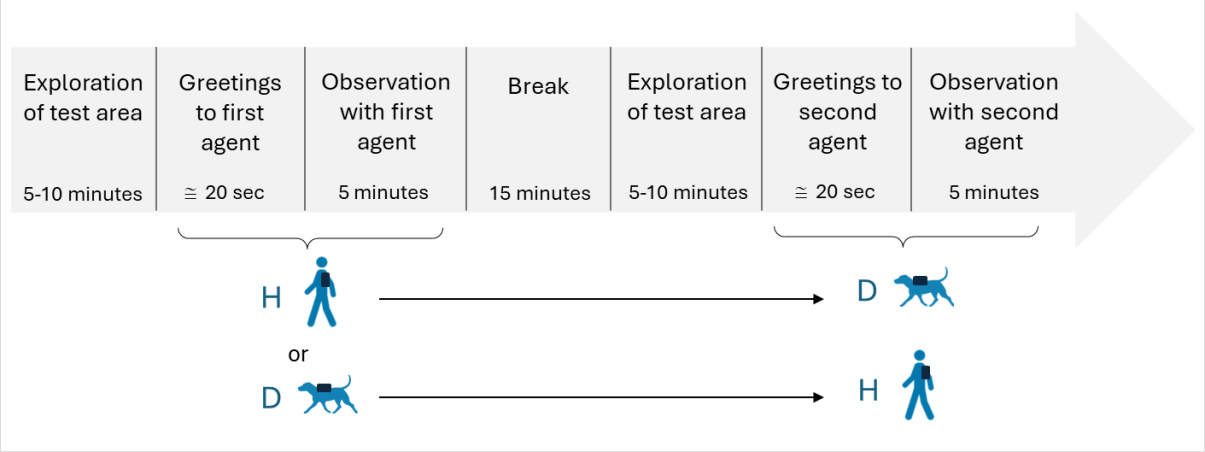


Figure 2. Chronology of experimental procedure. 10 dogs were first observed with H and then with D, the other 10 dogs were first observed with D and then with H.

Instructions to H

D received no instructions and was allowed to move freely in the testing area when with the dogs. H was unaware of the study's aim and hypotheses, but was given the following instructions prior to the experiment, so that the observations of the dogs with H would be comparable to the observations of the dogs with D: after entering the park, let the dog sniff you, extend your hand if you wish, then start walking whenever you want and keep your arms by your sides; do not play with the dog, do not talk to the dog but you can look at the dog and in the direction of E1 and the owner; explore the entire area, including where E1 and the owner are, using four paces: stillness, walking, trotting, and running, spending more time walking and standing still than trotting, and run very little. These instructions were derived from pre-tests conducted prior to the experiment, involving the observation of D with 6 dogs not part of the current study. Each dog was observed individually for 5 minutes with the D, in the park shown in Figure 1. A. These pre-tests were video recorded, and the D's behaviours (see Supplementary File 1) were coded by E1 and E2 using BORIS software (version 8.25.4, Friard and Gamba, 2016). H was not present during these pre-tests, E1 and the dogs' owner were present within the test area, E2 was outside the test area. The dogs and D wore harnesses but were not equipped with GPS.

Data analysis

We analyzed data from the 5-minute observations in R (version 4.4.1; https://www.R-project.org). We did not include the greeting phases in the analyses because they were solely intended for the dog and the agents to greet each other and were not relevant to the study, as individuals obviously were close and engaged in the same actions during these phases.

We first checked the locomotion and gaze behaviour of D and H during the 5-minute observations, using Linear Mixed Models (LMMs). To model agents' speed, we used the *glmmTMB* package, with a gaussian error distribution, and we included the type of agent (2 levels: D and H) as fixed effects. Since the position data were recorded every 0.25 seconds, there was high temporal dependence, so we included an autocorrelation structure of order 1 (AR1). We modeled agents' gaze behaviour towards the dogs using the *lme4* package, with the type of agent as fixed effect. In both models, dog ID was included as random effects.

To compare intra- and interspecific behavioural synchronization, we analyzed the following variables: the distance between the dog and the agent (location synchronization), the speed difference between the dog and the agent (activity synchronization), and body alignment (another measure of activity synchronization). Additionally, we measured the dog's gaze behaviour towards the agents, see the definitions of the variables in Table 1. A naïve coder, who did not know the purpose and hypotheses of the study, coded body alignment and gaze behaviour variables from the video recordings using the BORIS software. The coder was first trained on videos from a different experiment until their results matched those previously obtained. To assess inter-coder reliability, a second naïve coder analyzed a subset of 25% of the videos, yielding a strong correlation between the two coders (time the agent spent gazing at the dogs: $R^2 = 0.98$, $P < 0.001$; time the dogs spent gazing at the agent: $R^2 = 0.99$, $P < 0.001$; body alignment: $R^2 = 0.97$, $P < 0.001$).

To analyse the distance variable, we ran a Generalized Linear Mixed Model (GLMM) using the *glmmTMB* package, with a gamma distribution for errors and log link function. The speed difference was modeled with a GLMM using the *glmmTMB* package with a zigamma distribution for errors and log link function. We included an AR1 structure in these GLMMs. Body alignment and gaze behaviour were modeled with a LMM using the *lme4* package. In all (G)LMMs, the type of agent and the presence of another dog in the household (2 levels: yes and no) as well as the interaction between these two factors were included as fixed effects. We included dogs' sex and age as nuisance variables, and dog ID as random effects.

Model assumptions were graphically checked using the *DHARMa* package. For each model, we compared the full model with the corresponding null model (which included only the nuisance variables and random factors) using Likelihood Ratio Tests (LRT), with the *anova* function and the *chisq* argument. If the null-full model comparison was significant, we reported the estimates and standard errors (SE) of the full model, obtained using the *summary* function. We also provided 95% confidence intervals (95% CI), obtained using the *confint* function. Test statistics from Wald chi-square tests were calculated using the *Anova* function from the *car* package with Type 3 sum of squares. Where post-hoc comparisons were necessary, we used

the *emmeans* package with the Kenward-Roger approximation and Tukey corrections for multiple testing.

	Variable name	Variable definition	Data collection
Location synchronization	Distance between agent and dog	Distance in metre between the agent's back and the dog's back.	From GPS data, 2400 values for each dog (1200 for each agent).
Activity synchronization	Speed difference between agent and dog	Absolute difference in metre/second between the agent's speed and the dog's speed.	From GPS data, 2400 values for each dog (1200 for each agent).
	Body alignment	Time in seconds during which the dog's body and the agent's body were oriented in the same direction.	From video recordings, 2 value for each dog (1 for each agent).
Gaze behaviour	Gaze towards the agent	Time in seconds during which the dog's muzzle was oriented towards the agent	From video recordings, 2 value for each dog (1 for each agent).

Table 1. Definitions of the dependent variables.

Results

Locomotion and gaze behaviour of D and H

D and H did not differ significantly in their speed (LRT: $\chi^2 = 2.39$, df = 1, P = 0.122) or in their gaze behaviour towards the dogs (LRT: $\chi^2 = 1.04$, df = 1, P = 0.308).

Location synchronization

The null-full model comparison for the distance was significant (LRT: $\chi^2 = 14.10$, df = 3, P = 0.003). The distance was smaller when the dogs were with D than when they were with H (Table 2 and Figure 3).

Fixed effect	Estimate	SE	z value	95% CI	χ^2	P
Intercept	0.80	0.25	3.25	[0.32; 1.28]	10.59	0.001
Type of agent (H)	0.75	0.19	4.02	[0.38; 1.11]	16.19	<0.0001
Presence of another dog in the household (yes)	0.08	0.26	0.30	[-0.43; 0.58]	0.09	0.767
Type of agent (H): Presence of another dog in the household (yes)	-0.40	0.29	-1.35	[-0.97; 0.18]	1.83	0.176
Dog's age	0.04	0.04	0.96	[-0.04; 0.11]	0.93	0.336
Dog's sexe (male)	-0.19	0.18	-1.09	[-0.54; 0.15]	1.18	0.278

Table 2. Results of the GLMM of the distance. The predictors were dummy coded, with agent (D), presence of another dog in the household (no), and sex (female) being the reference categories. Estimate ± SE refers to the difference of the response between the reported level of this categorical predictor and the reference category of the same predictor.

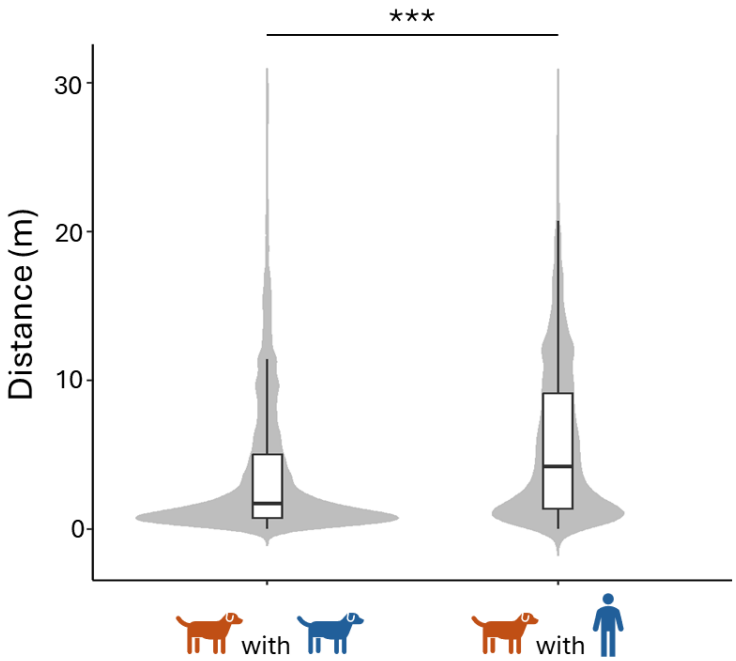


Figure 3. Effect of type of agent on location synchronization. D and H are depicted in blue, the dogs are depicted in brown. The distance between the dogs and D was significantly smaller than between the dogs and H. *** $P \leq 0.001$

Activity synchronization

The comparison between the null and full model for speed difference was significant (LRT: $\chi^2 = 9.57$, $df = 3$, $P = 0.023$). Analysis of the full model revealed a significant interaction between the type of agent and the presence of another dog in the household (Table 3). Post-hoc tests indicated that, for dogs not living with other dogs, the speed difference was smaller when the dogs were with D than when they were with H (Table 4 and Figure 4).

Fixed effect	Estimate	SE	z value	95% CI	χ^2	P
Intercept	-0.85	0.16	-5.19	[-1.17; -0.53]	26.97	<0.001
Type of agent (H)	0.40	0.12	3.35	[0.16; 0.63]	11.19	<0.001
Presence of another dog in the household (yes)	0.16	0.14	1.21	[-0.10; 0.43]	1.45	0.228
Type of agent (H): Presence of another dog in the household (yes)	-0.48	0.19	-2.57	[-0.85; -0.11]	6.58	0.010

Dog's age	-0.01	0.03	-0.21	[-0.06; 0.05]	0.04	0.835
Dog's sexe (male)	0.06	0.13	0.43	[-0.21; 0.32]	0.19	0.666

Table 3. Results of the GLMM of the speed difference. The predictors were dummy coded, with agent (D), presence of another dog in the household (no), and sex (female) being the reference categories. Estimate ± SE refers to the difference of the response between the reported level of this categorical predictor and the reference category of the same predictor.

Contrasts	Ratio	SE	95%CI	Z ratio	P
D no / H no	0.67	0.08	[0.50; 0.91]	-3.35	0.005
D no / D yes	0.85	0.85	[0.60; 1.20]	-1.21	0.624
D no / H yes	0.92	0.92	[0.57; 1.49]	-0.43	0.973
H no / D yes	1.26	1.26	[0.82; 1.96]	1.37	0.519
H no / H yes	1.37	1.37	[0.80; 2.37]	1.50	0.438
D yes / H yes	1.09	1.09	[0.75; 1.58]	0.68	0.939

Table 4. Post-hoc tests for the interaction between type of agent (D or H) and presence of another dog in the household (yes or no) on the speed difference variable.

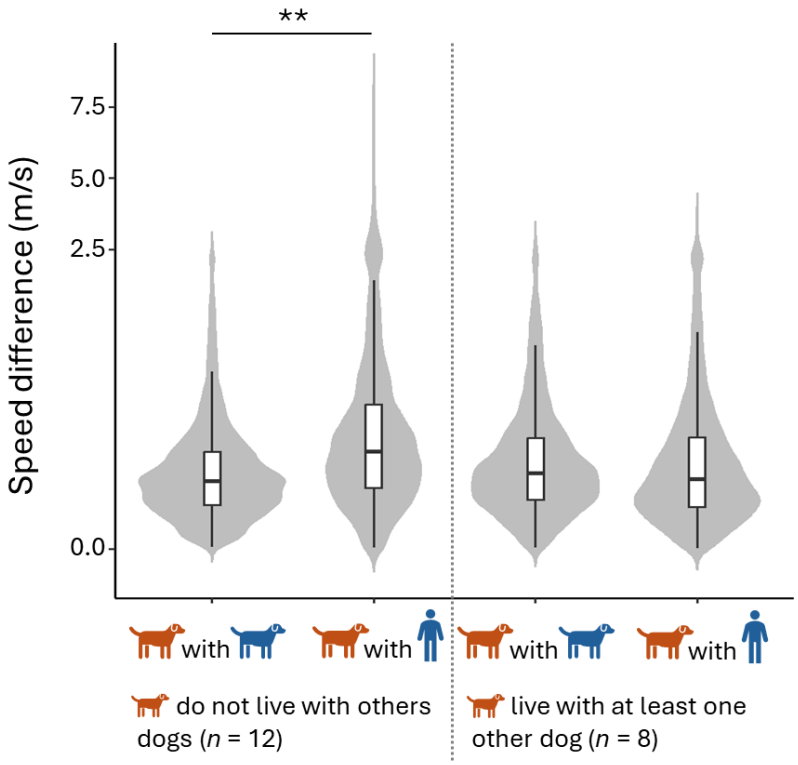


Figure 4. Effect of interaction between type of agent and presence of another dog in the household on speed difference. D and H are depicted in blue, the dogs are depicted in brown. For dogs that do not live with other dogs, the speed difference between the dogs and D was significantly smaller than between the dogs and H. Data exceeding 2.5 m / s were squashed. ** $0.001 \leq P \leq 0.01$

Regarding body alignment, the null-full model comparison was not significant (LRT: $\chi^2 = 2.52$, $df = 3$, $P = 0.472$), indicating that the variables of interest did not significantly improve the model fit. The dog and the agent's bodies were aligned for an average of 60.72 ± 26.44 seconds over the 5-minute observation period.

Gaze behaviour towards the agents

The null-full model comparison was not significant (LRT: $\chi^2 = 3.23$, $df = 3$, $P = 0.356$), indicating that the variables of interest did not significantly improve the model fit. The dogs spent 136.36 ± 7.66 seconds gazing at the agent over the 5-minute observation period.

Discussion

This study represents the first direct comparison of intraspecific and interspecific behavioural synchronization in dogs and is thought to provide key knowledge on processes underlying behavioral synchronization. We compared dogs' locomotor synchronization and gaze behaviour with a familiar conspecific (D) and with a familiar human (H), during

spontaneous movements in an outdoor setting. We hypothesized that dogs would synchronize more with D than with H and that they would display greater visual attention towards H. Our hypotheses were only partially confirmed, as our findings indicate that dogs displayed better location synchronization with D and better speed adjustment, but this latter effect was found only for dogs living without another dog in the household. We found no significant differences between the two experimental conditions in terms of body alignment or visual attention.

The closer distance between dogs and D, which aligns with our hypothesis, suggests a stronger proximity between conspecifics than between individuals from different species. Previous studies have reported lower proximity-seeking behaviours in shelter dog-caregiver dyads (Thielke & Udell, 2019) and pet dog-child dyads (Wanser et al., 2020) compared to dog-adult owner dyads. These differences were correlated with reduced synchronization levels in the two former dyads (Duranton et al., 2019b; Wanser et al., 2021). The enhanced location synchronization between dogs in our study may thus be attributed to stronger proximity-seeking behaviour between conspecifics. However, two studies have found that dogs seek proximity with an unfamiliar human more than with a cohabitant dog, except when the conspecific was their mother (Mariti et al., 2014, 2017). Future studies are thus needed to clarify links between exhibiting proximity-seeking behaviours, and behavioural synchronization in dogs.

Regarding activity synchronization, our findings indicate that dogs adjust their speed more effectively to that of a conspecific, but this ability is influenced by cohabitation with another dog. A likely explanation for the stronger speed synchronization between dogs is physical: similar locomotor patterns make it easier for individuals to synchronize. In humans, locomotor synchronization occurs spontaneously during walks but is less easily achieved when individuals have different step frequencies or leg lengths (Nessler et al., 2013). Similarly, locomotor synchronization occurs spontaneously in dogs walking with humans, but the quadrupedal versus bipedal difference likely makes speed synchronization less easily achieved between dogs and humans than between conspecifics. Interestingly, this applies only for dogs that do not live in multi-dog households, as dogs living with conspecifics were better at synchronizing their speed with the human compared to dogs living without conspecifics. As dogs in multi-dog households are more exposed to interspecific interactions, it is possible that this repeated exposure enhances the dogs' ability to adjust to human speed. This finding aligns with the role of experience in shaping behavioural synchronization, as noted in previous research (Duranton et al., 2022). Heyes (2010, 2016) proposed that behavioural synchronization develops when individuals perform an action while simultaneously observing others performing the same action, or when observing third parties performing synchronized actions. Our study is in line with this view, highlighting how daily experience influences dogs' behaviours towards humans and conspecifics.

Despite the closer proximity and the better speed adjustment with D for some dogs, we did not find a significant difference in body alignment with D and H, which was contrary to our expectations. A possible explanation is that during walks, dogs and humans have their bodies oriented in the same direction most of the time, but only one study has measured body alignment between dogs and humans (Wanser et al., 2021). The authors found that dogs spent about 30% of the time aligned with a child's body orientation during walks, and we found a 20% alignment rate in our study. Nevertheless, due to the lack of significant results, we cannot draw definitive conclusions about body alignment. Also, we did not find significant differences in dogs' visual attention between the two experimental conditions. It is possible that the increased attention towards humans described in previous literature(Cimarelli et al., 2019), may only manifest in specific contexts, such as unsolvable tasks, and not in free interactions without a specific goal. Once again, we cannot extend our interpretation further on this point given the non-significant results.

This study contributes to the growing body of research comparing intraspecific and interspecific cognition in dogs. While dogs possess highly developed social skills towards humans, due to their evolutionary history alongside them, these skills are also present in their intraspecific interactions and may even be stronger for certain components of behavioural synchronization. This aligns with the literature suggesting that dogs' social cognitive abilities are likely inherent to the species, with domestication facilitating the development of these abilities in interspecific contexts (Fugazza et al., 2018, 2023; Range & Virányi, 2013). Furthermore, the finding that cohabitation with a conspecific influences speed synchronization suggests that behavioural synchronization is flexible and shaped by life experiences. This also offers practical insights, such as the potential use of conspecifics to facilitate dogs' accommodation to novel and potentially threatening situations. It regularly happens that a familiar conspecific serve as a model, allowing a dog to adjust to their behaviour and feel more secure.

Like all studies, ours has some limitations. One potential bias stems from our sample population, which consisted of dogs accustomed to training and frequent interaction with conspecifics. Moreover, half of the dogs were herding breeds. Although we made this selection for methodological reasons, future studies should include other dog populations, this would help to generalize our findings. Conducting a similar study with shelter dogs, for example, would allow to examine the impact of social deprivation on their ability to synchronize with humans and with conspecifics. Additionally, the presence of the owner in the testing area was unavoidable in our study, as the absence of the owner significantly in pre-tests thoroughly reduced interactions between the dogs and the agents. Consequently, our protocol did not allow for observations of conspecific interactions without human presence. Furthermore, the use of

the same dog and human (D and H) for all dogs ensured comparable observations and effectively controlled for the effect of familiarity, an important social modulator of behavioural synchronization. However, the results could be different if other agents were used to play the roles of D and H. Replicating the protocol with dogs from the same household and a human household member, for instance, could extend our results and shed light on how the level of familiarity impact the comparison of intraspecific and interspecific behavioural synchronization.

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534

5. Exploration d'une manifestation comportementale de la résonance motrice chez le chien

L'interférence motrice, également appelée imitation automatique et largement étudiée chez l'humain, se produit lorsque l'exécution d'une action par un individu est perturbée par l'observation concomitante d'une action incongruente (voir Cracco et al., 2018 pour une revue). Cette perturbation peut se traduire par un temps de réaction pour effectuer l'action rallongé, pour ouvrir la main lorsqu'on observe une main qui se ferme, ou inversement, par exemple (Heyes et al., 2005) ou par une plus grande variation de mouvement dans l'espace, ce qui se traduit, par exemple, par une déviation du mouvement par rapport à l'axe vertical (ou horizontal) si le sujet doit bouger la main de haut en bas (ou de gauche à droite) pendant qu'il observe un mouvement de main de gauche à droite (ou de haut en bas) (Kilner et al., 2003). L'interférence motrice est ainsi une manifestation comportementale du couplage perception action : la perturbation mesurée traduit l'activation simultanée des représentations motrices de l'action exécutée et celles de l'action perçue (Cracco et al., 2018).

La copie de comportement du chien sur l'humain pourrait reposer sur la résonance motrice interspécifique, cependant il n'existe actuellement aucune preuve directe de cette hypothèse ; les études comportementales sur la synchronisation ne font que la suggérer. Démontrer l'interférence motrice lors de la perception d'actions humaines par des chiens permettrait de soutenir cette théorie. C'est dans ce cadre que nous avons conçu une expérience dans laquelle des chiens ont appris une action spécifique (poser leur patte sur une zone précise d'un tréteau). Nous avons supposé que l'interférence motrice se traduirait par des temps de réaction plus longs pour exécuter cette action si une action humaine incongruente en termes de hauteur était réalisée simultanément (poser la main plus haut ou plus bas que la zone apprise par le chien), par rapport à une action humaine congruente en termes de hauteur (poser la main à la même hauteur que la zone apprise par le chien). Nous avons également intégré des actions humaines absentes du répertoire comportemental des chiens (utilisation du coude au lieu de la main), en supposant que ces actions ne devraient pas induire d'interférence motrice, du fait de l'absence de représentations motrices associées chez les chiens. Enfin, nous avons exploré l'impact de l'expérience sensorimotrice, car des études chez l'humain ont montré que l'interférence motrice peut être abolie par un entraînement incongruent. Nous avons donc divisé les chiens en deux groupes : la moitié a été exposée à une répétition d'actions congruentes de la main, et l'autre moitié à une répétition d'actions incongruentes de la main. Nous avons émis l'hypothèse que l'interférence motrice ne serait plus visible chez ce second groupe après l'entraînement.

Les résultats ont révélé une tendance à des temps de réaction plus longs lorsque l'action humaine était incongruente en termes de hauteur. De manière intéressante, les temps de réaction étaient également rallongés pour les actions humaines du coude par rapport aux actions de la main. Après l'entraînement sensorimoteur, nous avons observé des temps de réaction significativement plus longs pour les actions humaines trop hautes par rapport aux actions congruentes, quel que soit le groupe expérimental. Par ailleurs, les chiens ayant reçu l'entraînement incongruent passaient plus de temps à observer les actions de la main que celles du coude.

Les effets de la hauteur d'une part, et de la partie du corps d'autre part, avant l'entraînement, suggèrent que le mouvement humain et la partie du corps utilisée sont traités chez le chien par des mécanismes distincts. Nous proposons que le traitement du mouvement humain pourrait être sous-tendu par la résonance motrice, tandis que l'effet de la partie du corps résulterait d'un décalage entre l'action prédite et l'action perçue. Finalement, cette étude représente une avancée majeure dans la compréhension des mécanismes de traitement des actions humaines par les chiens.

Article 6 : Lamontagne, A., Legou, T., Bedossa, T. & Gaunet. F. (in preparation). Temporary title: Investigating motor interference in dogs: Incongruent human actions interfere with canine task execution.

Investigating motor interference in dogs: Incongruent human actions interfere with canine task execution

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Abstract

It is well-established that dogs imitate human actions. An hypothesis posits that similar cognitive processes, including motor resonance, underly imitation in humans and dogs. Motor interference, a disruption in the execution of an action when observing an incongruent action simultaneously, has been widely investigated in humans and is a behavioural manifestation of motor resonance. This study is the first to explore motor interference at the interspecific level. Thirty-two highly trained dogs were taught to place their paw on a specific area of a support. Motor interference was then assessed by comparing their reaction times to perform their action when a human performed a congruent hand action (at the same height as learned by the dogs), an incongruent hand action (too high or too low) or an elbow action, which falls outside the dogs' motor repertoire. The results indicated a trend towards slower reaction times when dogs observed incongruent human actions in terms of height and a significant increase in reaction times when the human used their elbow rather than their hand. In the second part of the study,

the dogs underwent sensorimotor training that was either congruent (n = 16) or incongruent (n = 16) in terms of height. After training, dogs in both groups demonstrated significantly slower reaction times when observing a human action performed at a too-high height compared to congruent actions, and the previously observed effect of body part disappeared. Also, dogs in the incongruent training group spent more time gazing at hand actions than elbow actions. These findings prompt discussion on the cognitive processes involved in dog-human imitation, particularly the potential role of interspecific motor resonance and action prediction in the processing of human movement and human body part, respectively. Overall, this study contributes to our understanding of the cognitive underpinnings of imitation between two phylogenetically distant species.

Keywords: Automatic imitation, Canine, Motor interference, Motor resonance, Social Cognition

Highlights

- Incongruent height human actions disrupts the execution of paw actions in dogs.
- Actions performed with the elbow disrupt action execution in dogs, but only during the first test of motor interference.
- The effect of sensorimotor training on motor interference was not demonstrated in our study.
- Human movement and body part seem to be processed by distinct cognitive mechanisms in dogs compared to humans.

Introduction

Pet dogs hold a special place with humans due to their long history of domestication and their extensive interactions with humans from birth (Bergström et al., 2020; Range and Marshall-Pescini, 2022). Research over the last few decades has revealed that some social cognitive abilities commonly present at the intraspecific level, notably imitative skills, are also found in dogs during interactions with humans. Dogs are indeed capable of replicating human actions (Fugazza et al., 2019, 2023; Huber et al., 2009, 2018; Range et al., 2011; Topal et al., 2006) and synchronizing their behaviours with those of humans (Duranton et al., 2017, 2018; Heurlin et al., 2024; Lamontagne et al., 2023; Wanser et al., 2021). Studies have delved into the properties of these imitation skills, revealing that they are modulated by social factors, for instance the level of familiarity (Duranton & Gaunet, 2016; Duranton et al., 2019; Huber et al., 2022; Merola et al., 2012; Lamontagne et al. 2024a,b; Romero et al., 2013); that they depend on development and experience (Duranton et al., 2022; Madsen and Personn, 2013; Range et al., 2011) and that they occur even after a delay (Fuazza et al., 2016; Fugazza and Miklósi, 2014). However, the neurocognitive foundations of dogs' ability to copy human behaviours remain poorly explored. It has been suggested that this ability may be based on neurocognitive foundations analogous to those governing imitation in humans and other primates, specifically motor resonance (see Lamontagne & Gaunet, 2024 for a review). Motor resonance involves a correspondence between the sensory and the motor representations of an observed action, making the observer more inclined to perform the action themselves (Jeannerod, 2001; Prinz, 1997; Rizzolatti & Craighero, 2004; Guidali et al., 2023; Uithol et al., 2011). Recent fMRI studies have revealed analogies between the neural bases of action observation in adult dogs and humans, such as the involvement of the temporal lobe, while also highlighting differences, such as the involvement of the parietal lobe in humans but not in dogs (see Boch et al., 2024 for a review). However, the neural bases of more complex cognitive abilities such as imitation have not yet been studied in dogs. Consequently, the existence of motor resonance between dogs and humans remains hypothetical.

This hypothesis of interspecific motor resonance can be investigated by examining whether behavioural manifestations of motor resonance are found during dog-human interactions. One such manifestation is motor interference, also called automatic imitation or motor contagion. It has been widely studied in humans and occurs when the execution of an action is disrupted by the simultaneous observation of an incongruent action, due to the activation of the sensorimotor representations of that action (see Cracco et al., 2018 for a meta-analysis). In human adult and children studies, motor interference is evidenced when subjects perform an action while observing another person perform either the same or an incongruent action and have prolonged

reaction times to perform the action (Brass et al., 2001; Craighero et al., 2002; Chang et al., 2009; Heyes et al., 2005; Press et al., 2005) or increased spatial variance in movement execution (Bouquet et al., 2007, 2010; Kilner et al., 2003, 2007; Kupferberg et al., 2012; Marshall et al., 2011; Richardson et al., 2009) when observing an incongruent action compared to a congruent one. For example, subjects are slower to open (or close) their hands when observing a hand-closing (or hand-opening) action (Heyes et al., 2005). As another example, subjects performing sinusoidal arm movements deviate from their movement plane when observing a person performing incongruent movements (vertical movements during observation of horizontal movements or vice versa) (Kilner et al. 2003).

To date, no studies have specifically investigated motor interference in dog-human interactions. One study demonstrated that dogs needed more trials to reach a performance criterion when they were trained by being rewarded after observing and copying human action (using the same body part as the human to open a box) compared to when they were rewarded for performing the opposite action (using their paw to open the box while the human used their head, and vice versa) (Range et al., 2011). The results thus demonstrate the dogs' tendency to copy humans, and that repeated exposure to the demonstration of the opposite action is necessary to inhibit this tendency. The study therefore indicates that imitation facilitates dog training, which aligns with the hypothesis of motor resonance between dogs and humans, but it does not conclusively prove this hypothesis, nor does it provide evidence of motor interference in dogs: since the humans demonstrated the action before the dogs had to perform their own action, the study does not show any disruption in the dogs' execution of an action while simultaneously observing an incongruent human action. Also, Range et al. (2011) study does not include human actions outside of the canine behavioural repertoire, but motor resonance is possible only for actions within the observer's behavioural repertoire (Buccino et al., 2004; Paulus et al., 2011), as subjects cannot have motor representations of an action that they are not able to do. Further research is therefore warranted to provide more insight into the hypothesis of interspecific motor resonance, by testing motor interference in dogs when observing human actions within and without the canine behavioural repertoire.

Range et al. (2011) study had a second phase in which they showed that dogs who were trained to counterimit continued to do so in 70% of trials even when they were no longer rewarded for it but were rewarded for copying the human. The authors suggested that the experience received by this group of dogs created sensorimotor associations between the action performed and the opposite action, aligning with the Associative Sequence Learning (ASL) model proposed by Heyes (2001). This model posits that the connection between the sensory and motor representations of an action, which causes motor interference when observing an incongruent

action, is established through repeated experiences of observing and executing the action, and that these sensorimotor connections are modulated by training, thereby impacting motor interference (Heyes, 2001, 2010, 2016). Studies in humans have indeed shown that training subjects to perform an action while observing an incongruent action reduces or abolishes motor interference (Bardi et al., 2015; Capa et al., 2010; Catmur and Heyes, 2019; Catmur et al., 2007, 2009; Cook et al., 2012; Heyes et al., 2005; Press et al., 2007; Roberts et al., 2016). In Heyes et al. (2005) study, for instance, subjects trained to open their hand while observing a hand closing, and to close their hand while observing a hand opening, showed no subsequent motor interference: their reaction times did not differ between congruent and incongruent trials after training. While numerous studies support the ASL model in humans, its exploration in dogs remains limited, with Range et al. (2011) being the only study to investigate this model in dogs to our knowledge.

In the present study, we investigated for the first time whether motor interference occurs when dogs observe a human action while performing their own. This has never been tested before, and demonstrating motor interference would provide indirect evidence of interspecific motor resonance. This study thus aims to 1) determine if a human incongruent action can interfere with the execution of a dog's action, and 2) explore if this motor interference can be modulated by sensorimotor training, as suggested by the ASL model. This would not only enhance our understanding of canine cognition but also of the cognitive processes related to imitation between species that are phylogenetically distant yet living in the same environment, thus providing new insights into the evolutionary roots of social cognition.

Thirty-two highly trained dogs learned a specific action: placing their paw on a specific part of a trestle upon hearing a sound signal, without human demonstration. We chose a paw-based action because dogs should have experiences related to both observing and performing this type of actions with humans (for example, when dogs lift their paw for the "give paw" command, with the human extending their hand simultaneously) (Range et al., 2011). Following the hypothesis of interspecific motor resonance, motor interference should occur when dogs observe incongruent human actions while performing their own. To test for this, we adapted human protocols involving arm movements. After the training process, we measured motor interference by comparing the dogs' reaction times to perform their action when, simultaneously with the sound signal, a human experimenter performed a hand action that was either congruent in height (placing their hand on the other part of the trestle at the same height as that learned by the dog) or incongruent in height (placing their hand on the other part of the trestle at a higher or lower height than that learned by the dog). Given the limited horizontal range of dogs' paws, we used only the vertical axis in our test. We expected that motor

interference would manifest as longer reaction times for the incongruent hand actions compared to the congruent hand action. Additionally, since motor resonance is possible only for actions within the observer's behavioural repertoire, we expected that there would be no motor interference if the experimenter's action was performed with the elbow instead of the hand, as dogs cannot bend their elbows to place them on the trestle. Dogs' reaction times would thus be longer for incongruent hand actions compared to actions performed with the elbow. We also measured dogs' gaze behaviour towards the experimenter and towards the experimenter's action to consider potential biases in the dogs' visual attention according to the different types of action.

Additionally, to investigate the link between motor interference and sensorimotor training, dogs were then split into two experimental groups. For half of the dogs (*congruent training, n* = 16), the experimenter performed the congruent hand action simultaneously with the dog's action 12 times in a row. For the other half of the dogs (*incongruent training n* = 16), the experimenter performed an incongruent hand action simultaneously with the dog's action 12 times in a row. A new test of motor interference was then conducted, i.e. with congruent and incongruent hand or elbow actions. Following the ASL model, we expected to observe motor interference only for dogs in the *congruent training* group: their reaction times would be greater for incongruent hand actions than for congruent hand action and elbow actions; while motor interference would be faded by sensorimotor experience for dogs in the *incongruent training* group, meaning no significant differences between congruent and incongruent hand or elbow actions. Dogs' gaze behaviour towards the experimenter and towards the experimenter's action was again recorded to consider potential biases in the dogs' visual attention according to the different types of action.

Material and Method

Ethical note

This study was conducted in accordance with the Declaration of Helsinki and its latest revision in 2013, the regulations of France where the research was conducted, and the institutional guidelines of Aix-Marseille University. All dog owners signed a consent form. All the dogs were in good health, with no signs of aging or behavioural problems, based on information from the owners and observations by the experimenter. The experiment took place at the owners' home between June 2023 and January 2024. The same experimenter carried out all the learning and testing sessions. In the first session, the experimenter explained the experimental protocol to the owner while setting up the equipment. The dog got acquainted with the apparatus and the

experimenter during this time, i.e. approximately 10 minutes. The experimenter then spent an additional 10 minutes becoming familiar with the dog through play and petting. No physical restraint was imposed on dogs at any time. During all sessions, the dogs were free to move and were given breaks every 5 to 10 minutes of work or whenever they showed signs of disinterest, to prevent fatigue or stress. During breaks, the dogs could play and interact with their owner and with the experimenter.

Participants

Thirty-two dogs of various breeds or crossbreeds participated in the experiment (dog breeds are in Table S1 in the Supplementary File). Sample size was chosen beforehand, based on previous research using similar methodologies (Kilner et al., 2007; Heyes et al., 2005; Range et al., 2011). Dog owners were recruited through posters in dog club and posts on social media platforms. The dogs were aged 1 to 10 years old (mean ± SD = 3.3 ± 2.3 y.o.). All the dogs had a high level of training, with at least one session per week in activities such as agility, education, obedience, whooper or dog dancing. The test of motor interference occurred after the completion of the process of learning a specific task. After this test, the dogs were randomly assigned to one of two experimental groups: *congruent training* (n = 16, counterbalanced for sex) and *incongruent training* (n = 16, counterbalanced for sex). Motor interference was tested again directly after the training.

Apparatus

The experimenter and the dog were positioned in front of a trestle (Figure 1). The trestle stood 74 cm high and 73.5 cm wide, and it was equipped with 8 wooden brackets, each measuring 14 cm x 3.2 cm x 3.2 cm (Figure 2. A). These brackets were covered with thin metal squares and connected to the central box. The brackets were arranged in 2 columns of 4, located on the left and right sides of the trestle, with each bracket spaced 14 cm apart and aligned in height with its corresponding bracket on the opposite side (Figure 2.A). The bearing surfaces of the lowest and highest brackets were positioned 21.5 cm and 62.5 cm above the ground, respectively.

A capacitive sensing system was integrated to detect contact with the metal surfaces. This system operated by sensing changes in electrical capacitance when a conductive object, such as a hand or paw, touched the metal-covered brackets. It was connected to a measurement and control system based on an Arduino MEGA 2560. Each time the experimenter pressed the button (Figure 1. A), a number (1, 2, 3 or 4) with the indication “hand” in French (Figure 2. B)

or “elbow” in French (Figure 2. C) appeared on a 9.6" OLED 128*64 display screen in the central box (Figure 2.A). On another screen, a visual message “GO” appeared in one out of two times the button was pressed (Figure 2.B and 2. C), and the sound signal was emitted from the speaker on the central box. The capacitive sensing system detected changes in capacitance, allowing for recording directly on the computer the time in milliseconds between the sound signal and the contact on the metal-covered brackets. The experimenter could press the button again either 4 seconds after the contacts were detected, or after 10 seconds if no contact was detected.

During learning sessions, the experimenter ignored the screens and used the button to train the dogs to place their paw on one of the metal-covered brackets in front of them (either No.2 or No. 3) when hearing the sound signal. During the tests of motor interference, the experimenter referred to the screens to place their hand or elbow on the indicated bracket number when the instruction “GO” appeared. Prior to the test, the experimenter used a switch to adjust the bracket numbers according to the bracket learned by the dog: the screen displayed numbers 1 to 3 if the dog had learned to place its paw on bracket No. 2, or numbers 2 to 4 if the dog had learned to place its paw on bracket No. 3.

Additionally, a metal-covered bracket attached to a stick was used for the initial steps of the learning process (Figure 2.D). All training and test sessions were videotaped with a digital camera mounted on a tripod (Figure 1).

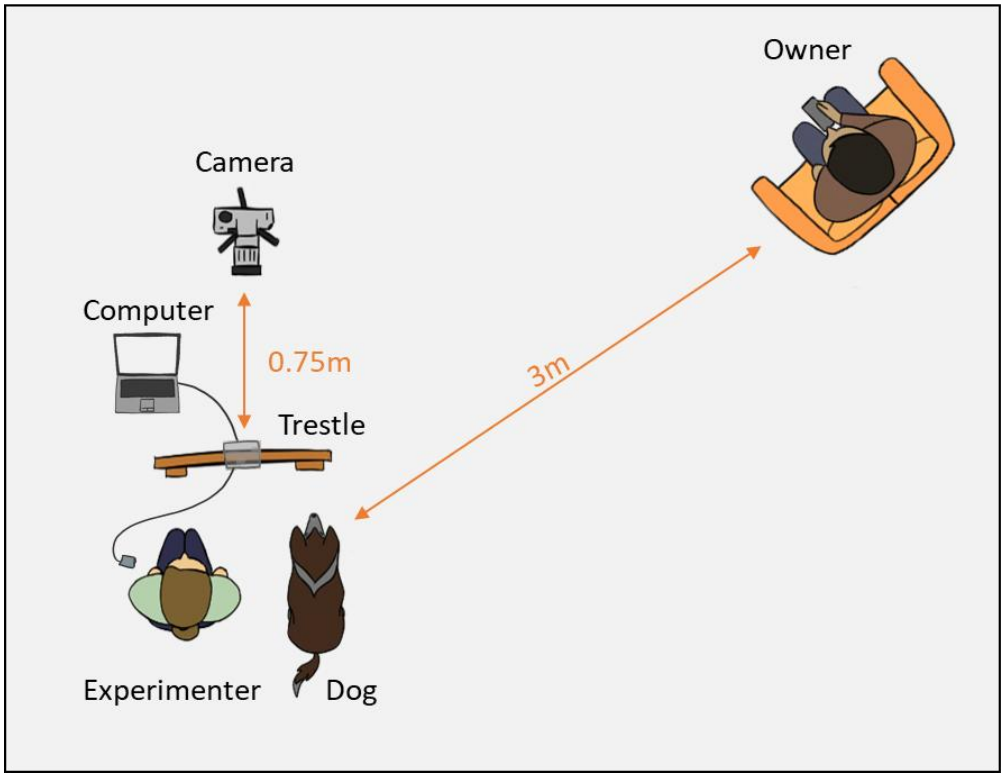


Figure 1. Experimental settings.

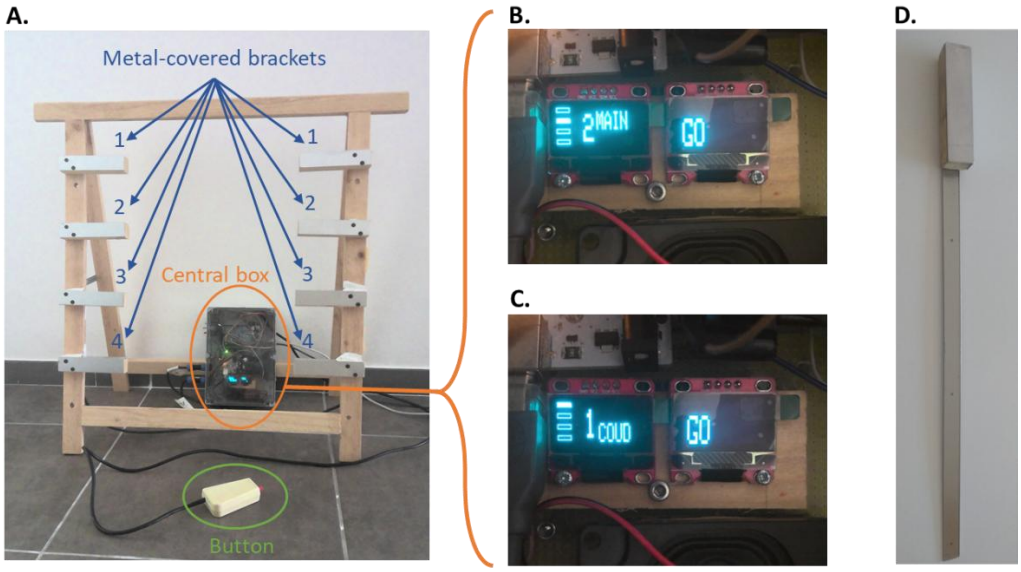


Figure 2. Material used for the experiment. The setup included a trestle equipped with 8 metal-covered brackets connected to the central box, along with a button also connected to the central box (A). Display screens on the central box were used during tests of motor interference (B, C), and a metal-covered bracket attached to a stick was used for the initial steps of the learning process (D).

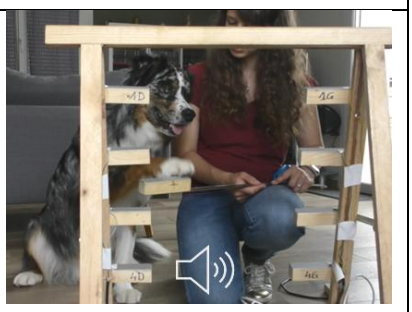
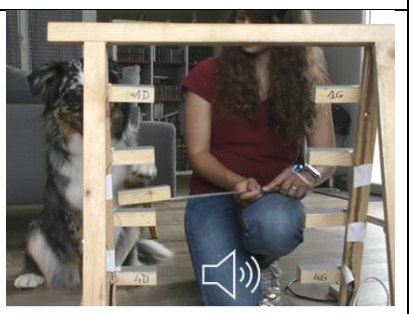
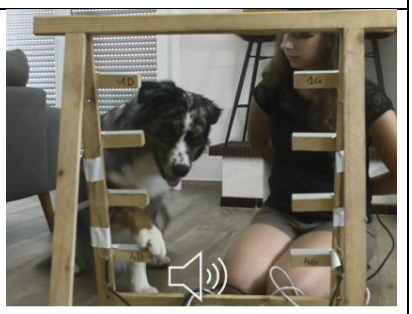
Experimental procedure

- *Preliminary training*

The dogs were initially shaped to place their paw on a specific bracket on the trestle after hearing the sound signal. For half of the dogs, the experimenter was on the left side throughout the procedure, as shown in Figure 1. For the other half, the experimenter was on the right side. The learning process consisted of several steps (see Table 1), using positive reinforcement with food rewards and praise from the experimenter. The owners supplied the food rewards to the experimenter. To progress through each learning step, the dog needed to perform the task correctly three times in a row, except for steps 6 and 7. For these steps, the criterion was that the dog performed the task correctly 10 times out of 12 attempts. We chose this threshold based on previous studies showing that a fixed criterion of 80-85% performance significantly decreases the probability of performing an action correctly by chance (Range et al 2011, Fugazza et al. 2015, Autier-Dérian et al. 2013). We did not apply this threshold for steps 1 to 5 because they were merely steps towards the final learning goal, and the criterion of three consecutive correct performances allowed for quicker progression to the next steps. The experimenter could help the dogs with referential signals but did not demonstrate the required actions at any point during the preliminary training. During steps 1 to 4, the experimenter held

the stick, and in steps 5 to 7, as the stick was no longer used, the experimenter kept their arms behind their back, holding the button. Throughout steps 3 to 7, when the experimenter pressed the button to emit the sound signal, they maintained a neutral facial expression, remained silent and motionless, and directed their gaze towards the dog's side of the trestle rather than directly at the dog. This allowed them to observe whether the dog correctly performed the task and to rewarded it accordingly. After each attempt, the experimenter instructed the dog to return to its initial position (sitting and waiting in front of the trestle) to repeat the task, or gave the dog a 10-minute break if it had successfully completed a learning step, had been working for 5 to 10 minutes or showed signs of inattention or disinterest (looking away, standing up or moving away from the experimental zone, alternating gaze between the experimenter and something other than the trestle). Dogs could interact with their owner and play with the experimenter only during breaks. If a dog struggled with a new step, the experimenter would revert to a previous step to provide additional practice.

After 30 to 45 minutes, meaning an average of 15-20 minutes of actual work, depending on the dog's attention and stamina, the learning session was stopped irrespective of the step the dog had reached. In the subsequent session, held 3 to 10 days later, the experimenter resumed training from the step achieved in the previous session. The intervals between learning sessions depended on the owners' availability and were based on similar intervals used in previous studies involving learning protocols in dogs (Meyer & Ladewig, 2008; Range et al., 2011). The dogs completed the learning process in 2 to 6 sessions (mean ± SD = 3.6 ± 1.0, see the dogs' learning progression in Table S2 in the Supplementary File). During the last steps of the learning process, the dogs had to place their paw on the same bracket – either No. 2 or No. 3, successfully in 10 out of 12 attempts. At the end of the training, all but one dogs had learned to place their paw on the bracket No. 3, meaning only one dog learned to place their paw on the bracket No. 2. Each dog eventually used its preferential paw consistently to perform their action. Of the 32 dogs, 20 dogs (11 females and 9 males) used their right paw – 18 had right-handed owners, 1 had a left-handed owner, and 1 had an ambidextrous owner. The other 12 dogs (5 females and 7 males) used their left paw – 4 had left-handed owners, and 8 had right-handed owners.

Step No.	Task	Success criteria to move to the next step	Ilustration
1	Sit in front of the trestle and next to the experimenter.	Perform the task correctly three times in a row.	
2	Sit in front of the trestle and place the paw on the metal-covered bracket attached to the stick held by the experimenter.	Perform the task correctly three times in a row.	
3	Sit and wait in front of the trestle and after hearing the sound signal, place the paw on the metal-covered bracket attached to a stick held by the experimenter.	Perform the task correctly three times in a row.	
4	Sit and wait in front of the trestle and after hearing the sound signal, place the paw on the metal-covered bracket attached to a stick held by the experimenter against the trestle, between brackets No. 2 and No. 3.	Perform the task correctly three times in a row.	
5	Sit and wait in front of the trestle and after hearing the sound signal, place the paw on one of the brackets fixed on the trestle (No. 4 in the illustration).	Perform the task correctly three times in a row.	

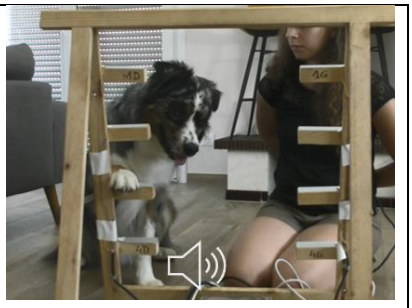
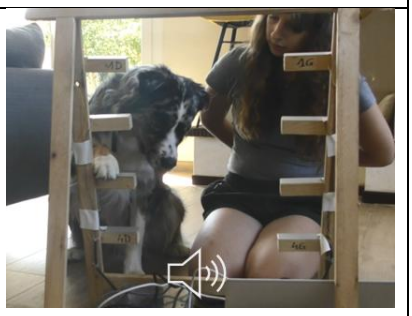
6	Sit and wait in front of the trestle and after hearing the sound signal, place the paw on bracket No. 2 or No. 3, whichever the dog had most frequently used (No. 3. in the illustration).		
7	Sit and wait in front of the trestle and after hearing the sound signal, place the paw the dog had most frequently used on the learned bracket (No. 2 or No. 3). In other words, although the previous step was reached, we reinforced the paw preferentially used (Right paw on bracket No. 3 in the illustration)		

Table 1. Steps of the learning process and success criteria to move to the next learning step.

- *Test of motor interference*

Just before the test of motor interference, the experimenter ensured that the final learning step was anchored by verifying that the dog placed its preferential paw on the learned bracket after hearing the sound signal at least 10 times out of 12 attempts. Following this verification, the test of motor interference started. It consisted of 36 trials, each trial began by the sound signal prompting the dog to do the action, as in the final step of the learning process. Every two trials, "go" appeared on the screen along with the emission of the sound signal, prompting the experimenter to execute the indicated action: they used either their hand or their elbow to perform a congruent or incongruent action in terms of height (see Figure 3 for the 7 experimental conditions). The experimenter used the arm corresponding to the dog's preferential paw (right arm if the preferential paw was the right one, left arm if the preferential paw was the left one). There was a trial without human action (no "go" on the screen) every two trials to prevent dogs from being accustomed to the human doing an action. Each human action in term of height was performed in total three times with the hand and three times with the elbow, in a randomized order (see Figure 4). During trials, the experimenter did not look

directly at the dog but looked at the dog's side of the trestle to see what the dog was doing. Each trial ended when the experimenter moved to give a food reward if the dog successfully placed its paw on the learned bracket or when the experimenter asked something else to the dog (lie down, up, stay and go take it) if the dog placed its paw elsewhere or did nothing for 10 seconds. The dog was then asked to go back to the initial position (sit and wait in front of the trestle) before starting the next trial. A 10-minute break was given to the dog after every 5 minutes of work, i.e. approximately every 12 trials. The dogs could interact with their owner during breaks.

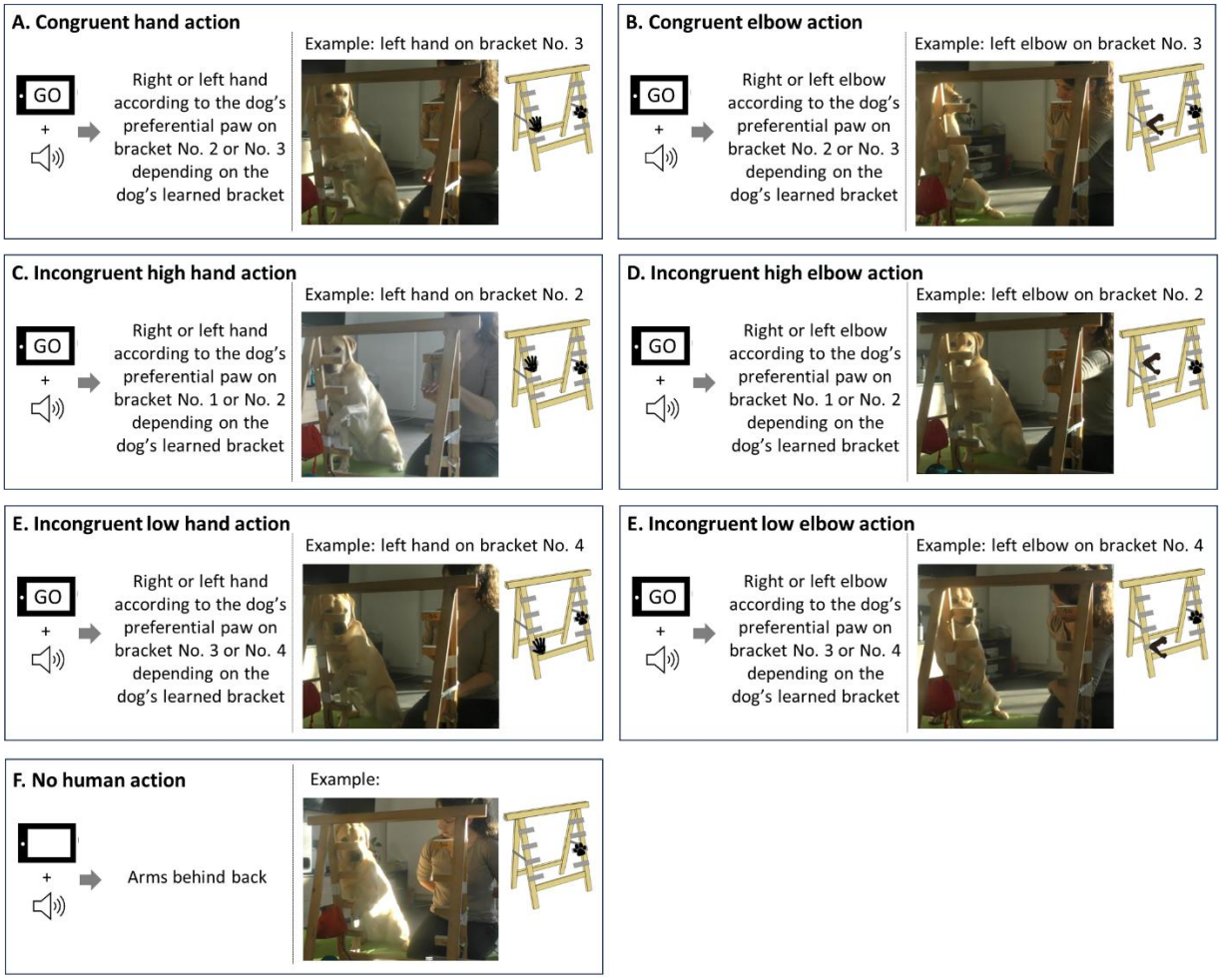


Figure 3. The 7 experimental conditions during the tests.

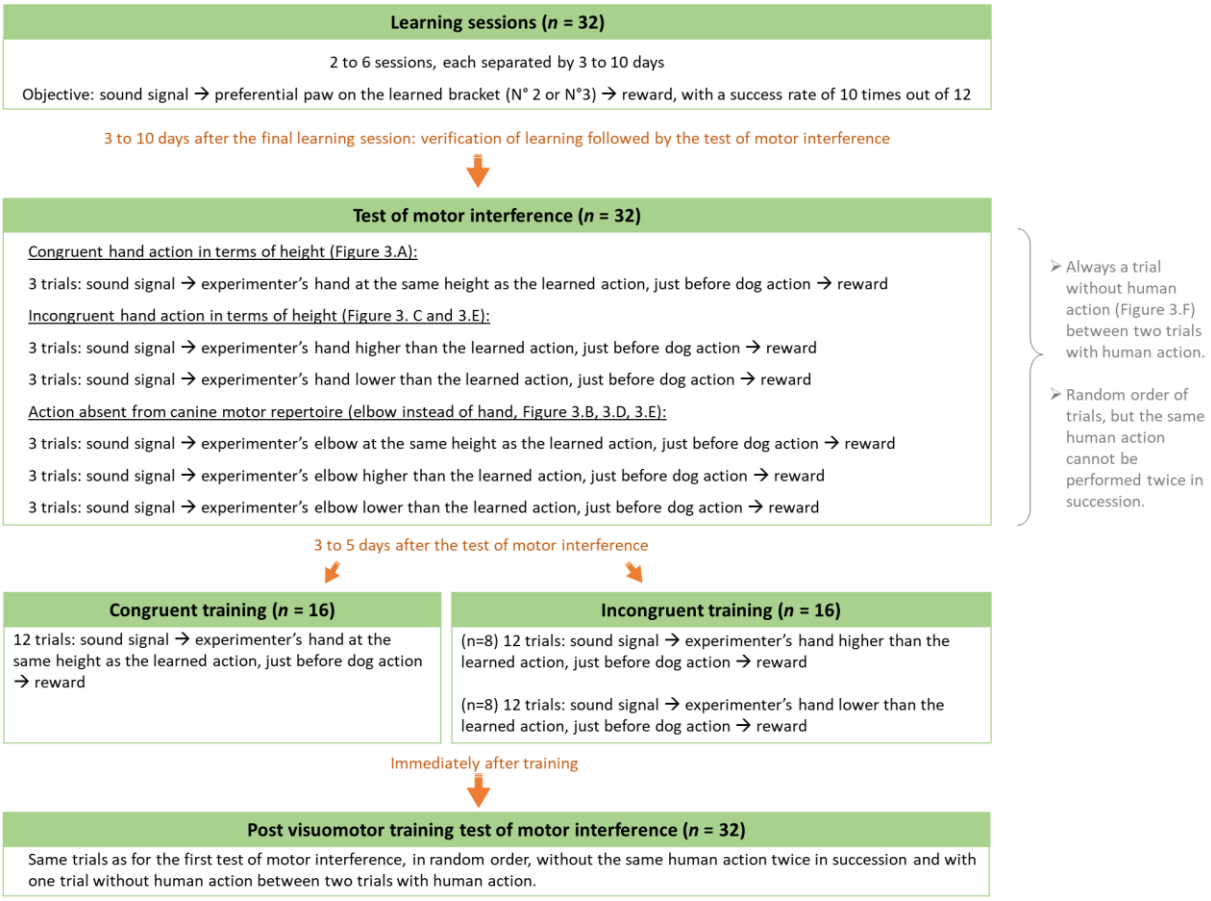


Figure 4. Experimental procedure. During the learning sessions, the experimenter taught to the dogs to place their paw on metal-covered bracket No. 2 or No. 3, the one the dogs had used most. During the test of motor interference, the experimenter conducted a series of trials in which they placed their hand or elbow on the trestle simultaneously with the sound signal in every two trials. Dogs were then split in two experimental groups and motor interference was tested again after a congruent or incongruent training.

- *Test of the effect of visuomotor training on dog's behavioural response*

The visuomotor training occurred 3 to 5 days after the first test of motor interference. Half of the dogs (n = 16) were exposed to a repetition of the congruent hand action (*congruent training* group): the experimenter performed the congruent hand action (Figure 3. A) for 12 trials in a row. The other 16 dogs were exposed to a repetition of an incongruent hand action (*incongruent training* group): the experimenter performed the incongruent high hand action (Figure 3. C) for 8 dogs, and the incongruent low hand action (Figure 3. E.) for the other 8 dogs, for 12 trials in a row. Immediately after the visuomotor training, a test of motor interference was conducted for all dogs. Exactly as for the first test, it consisted of 36 trials with 7 experimental conditions (Figure 3), with each human action in term of height performed three times with the hand and three times with the elbow, in a randomized order, and with a trial without human action following each trial with a human action. As in the first test, each trial ended when the

experimenter moved to give a food reward if the dog successfully placed its paw on the learned bracket or when the experimenter asked something else to the dog if the dog placed its paw elsewhere or did nothing for 10 seconds; and 10-minute breaks were given to the dog after every 5 minutes of work.

Great care was taken to avoid visual or acoustical cues from the experimenter during the tests. The experimenter was trained prior to the experiment to follow the indications on the screens and to move only their arm when indicated, avoiding any other movements or cues. Moreover, video recordings were checked by a blind coder for possible cueing, ensuring that the experimenter kept a neutral facial expression, and moved only their arm when required. The coder also verified that the experimenter rewarded the dogs consistently across all trials.

Variables and data analysis

To investigate motor interference in dogs, we defined three dependent variables (Table 2): dogs' reaction time to perform their action, dogs' gaze towards the human, and dogs' gaze towards the human action. Since dogs' gaze behaviour variables were proportions of time during trials, a blind coder, unaware of the hypotheses and purpose of the study, used Boris software (version 8.25.4, Friard and Gamba, 2016) to record the end of each trial, i.e. the timeframe when the experimenter either moved to give a food reward if the dog successfully placed its paw on the learned bracket or asked something else to the dog if the dog placed its paw elsewhere or did nothing for 10 seconds. The exact timeframes of the sound signal were obtained using Audacity software (version 3.4.2, https://www.audacityteam.org/). The coder then recorded for each trial the dogs' gazing behaviours from the sound signal to the end of the trial. The coder received prior training using videos not from this experiment. To ensure coding reliability, another naive coder coded a subset of 20% of the videos, and inter-rater reliability was assessed using Pearson correlation. A high level of correlation confirmed the coding reliability (time spent gazing at experimenter: $R^2 = 0.99$, $P < 0.001$; time spent gazing at human action: $R^2 = 0.98$, $P < 0.001$; length of trials: $R^2 = 0.99$, $P < 0.001$).

We conducted our analyses using R (version 4.4.1, http://www.r-project.org) to investigate whether human actions interfere with dogs performing their learned action. We first checked whether the presence of a human action (within-subject variable with 2 levels: action present, no human action) affected the dogs' reaction time. We ran a Cox Mixed Model (CMM) using the *coxme* package, with dogs' reaction time as the response, and presence of human action as the predictor. We then focused on trials involving a human action and we ran another CMM using the *coxme* package, with reaction time as the response and the following variables as

predictors: human body part (within-subject variable with 2 levels: hand, elbow), height of human action (within-subject variable with 3 levels: same height as the learned action, higher than the learned action, lower than the learned action), and the interactions between these variables.

Dogs' gaze behaviours during trials involving a human action were analysed with Generalized Linear Mixed Models (GLMMs), using the *glmmTMB* package, with a beta distribution for errors. The GLMMs included human body part, height of human action, and the interactions between these variables as predictors.

Dependent variable	Definition
Reaction time	Time in ms between the sound signal and the contact of the dog's paw on the bracket, obtained from the capacitive system.
Gaze towards human	Proportion of time spent by the dog with its muzzle oriented towards the head or torso of the experimenter during the trial, obtained from video recording coding.
Gaze towards human action	Proportion of time spent by the dog with its muzzle oriented towards the hand or elbow of the experimenter (depending on the action performed) during the trial, obtained from video recording coding.

Table 2. Definition of the dependent variables

We used the same variables (Table 2) for the test of motor interference following the visuomotor training. We first checked whether the presence of a human action affected the dogs' reaction time, as in the first test of motor interference, running a CMM using with human action as predictor. We then analyzed dogs' reaction time in trials with a human action using a CMM, with training type (between-subject variable with 2 levels: congruent training, incongruent training), human body part, height of human action, and the interactions between these variables as predictors. Dogs' gaze behaviours during these trials were analysed with GLMMs, with a beta distribution for errors, and we included training type, human body part, height of human action, and the interactions between these variables as predictors.

In all analysis, we included dog sex and age as nuisance variables, and dog ID as random effects. In CMMs, we applied a cause-specific hazard approach (Austin et al., 2016), treating trials during which dogs did not perform the learned action (i.e., did nothing or placed their paw

elsewhere) as censored observations. The results of the CMMs for the effects of the independent variables on the competing event of placing the paw elsewhere are provided in the last section of the Supplementary File.

Model assumptions were graphically checked using the *cox.zph* function in the *survival* package for CMMs, and the *DHARMa* package for GLMMs. For all models, we assessed whether the full model significantly differed from the corresponding null model (which included only nuisance variables and random factors) via Likelihood Ratio Test (LRT), using the *anova* function with the *chisq* argument. We provided $\chi 2$ and P-values of LRT. For significant null-full model comparisons, we reported from the *summary* function the estimates (β) with standard errors (SE) for full-GLMMs, and hazard ratio ($HR = \exp(\beta)$) for full-CMMs. We also reported 95% confidence intervals (95% CI), obtained using the *confint* function, and the $\chi 2$ and p-values from the Wald chi-square tests calculated using the *Anova* function from the *car* package with Type 3 sum of squares. Where needed, we performed post-hoc comparisons by using the *emmeans* package with the Kenward-Roger approximation and Tukey corrections for multiple testing.

Results

Test of motor interference

Dogs performed the learned action in 1008 of 1152 trials (i.e. in 88 % of all trials; see Table S3 in the Supplementary File for a full description on dogs' responses).

The presence of a human action affected the dogs' reaction times (full model vs. null model comparison: $\chi^2 = 160.75$, df = 1, $P < 0.0001$; effect of action: $\chi^2 = 164.26$, df = 1, $P < 0.0001$; HR = 2.34, 95%CI = [2.05; 2.66], z = 12.82). The CMM did not reveal an effect of dog sex ($\chi^2 = 0.10$, df = 1, P = 0.756; HR = 1.06, 95%CI= [0.75; 1.50], z = 0.31) and dog age ($\chi^2 = 0.57$, df = 1, P = 0.451; HR = 1.03, 95%CI = [0.95; 1.11], z = 0.75). The dogs had longer reaction time to execute the learned action when the experimenter performed an action (506 out of 576 trials, 2148.10 ± 68.81 ms) than when there was no human action (502 out of 576 trials, 1016.31 ± 48.14 ms). The reaction time for the experimenter to perform their action (576 trials) was 532.34 ± 9.81 ms.

Considering only trials with a human action (576, of which the learned action was executed in 506 trials), the full model of dogs' reaction time significantly differed from the null model ($\chi^2 = 21.95$, df = 5, $P < 0.001$). The full CMM revealed an effect of height of human action and an effect of human body part on dogs' reaction time, but we found no significant interaction

between these two factors (Table 3). Dogs took longer to perform their action when the human used their elbow compared to their hand (Figure 5. A). Regarding the effect of height of the human action, post-hoc tests indicated a trend: same height as the learned action vs higher: ratio ± SE = 1.28 ± 0.14, 95% CI = [0.99; 1.66], z ratio = 2.22, P = 0.068; same height as the learned action vs lower: ratio ± SE = 1.26 ± 0.14, 95% CI = [0.97; 1.63], z ratio = 2.10, P = 0.091; higher vs lower: ratio ± SE = 0.99 ± 0.11, 95% CI = [0.76; 1.28], z ratio = -0.13, P = 0.990. This suggests a tendency of shorten reaction times to perform the learned action when there was a congruent human action compared to incongruent human actions (Figure 5. B).

Fixed effect	HR	z	95% CI	χ^2	P
Height (higher)	0.71	-2.19	[0.52; 0.97]	6.69	0.035
Height (lower)	0.70	-2.25	[0.52; 0.96]		
Human body part (elbow)	0.61	-3.24	[0.45; 0.82]	10.51	0.001
Height (higher): human body part (elbow)	1.21	0.85	[0.78; 1.76]	1.28	0.527
Height (lower): human body part (elbow)	1.27	1.07	[0.82; 1.96]		
Dog sex (male)	1.19	0.74	[0.76; 1.86]	0.55	0.459
Dog age	1.02	0.39	[0.92; 1.13]	0.15	0.696

Table 3. Results of the CMM for dogs' reaction times in trials with a human action. The predictors were dummy coded, with height (same height as the learned action) and human body part (hand) being the reference categories. HR refers to the estimates of the ratio of the hazard rate for the reported level of a predictor versus the reference category of that predictor.

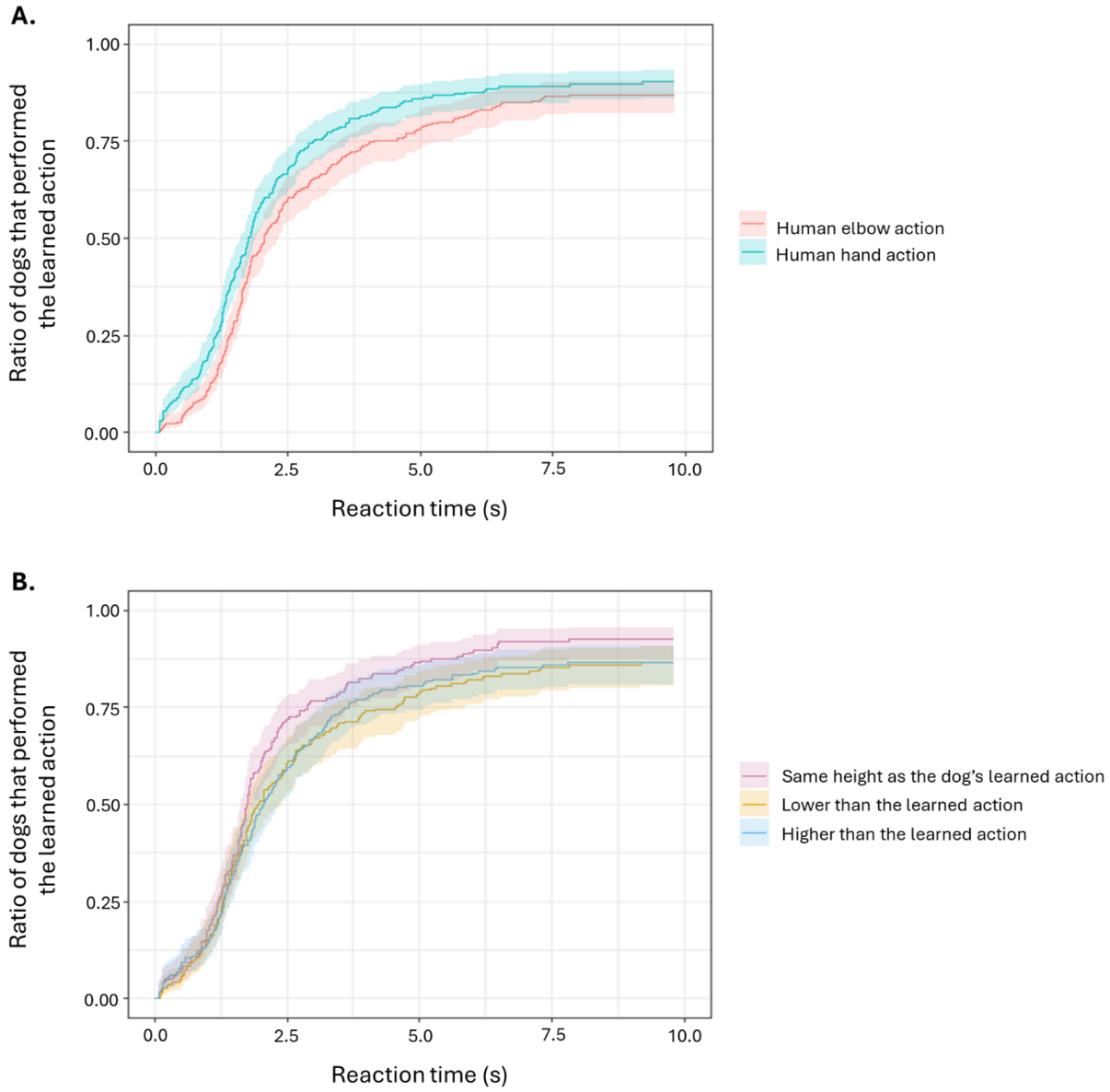


Figure 5. Proportion of dogs performing the learned action according to time during the test of motor interference, for both human body parts (A) and for each height of human action (B). Shading ± 95% CI.

Regarding dogs' gazing behaviour during trials with a human action (576 trials), dogs spent 40.70 ± 1.01 % of trial time gazing at the human action, with no effect of the variables of interest (full model vs. null model comparison: $\chi^2 = 6.64$, df = 5, P = 0.249), and 6.03 ± 0.49 % of trial time gazing at the human, with no effect of the variables of interest (full model vs. null model comparison: $\chi^2 = 3.15$, df = 5, P = 0.677).

458 *Test of the effect of visuomotor training on dog's behavioural response*

459 Half of the dogs underwent congruent training, while the other half underwent incongruent
460 training. Dogs performed the learned action in 86% (332/384) of the trials during this training
461 (see Table S4 of the Supplementary File for detailed responses of the dogs during training).

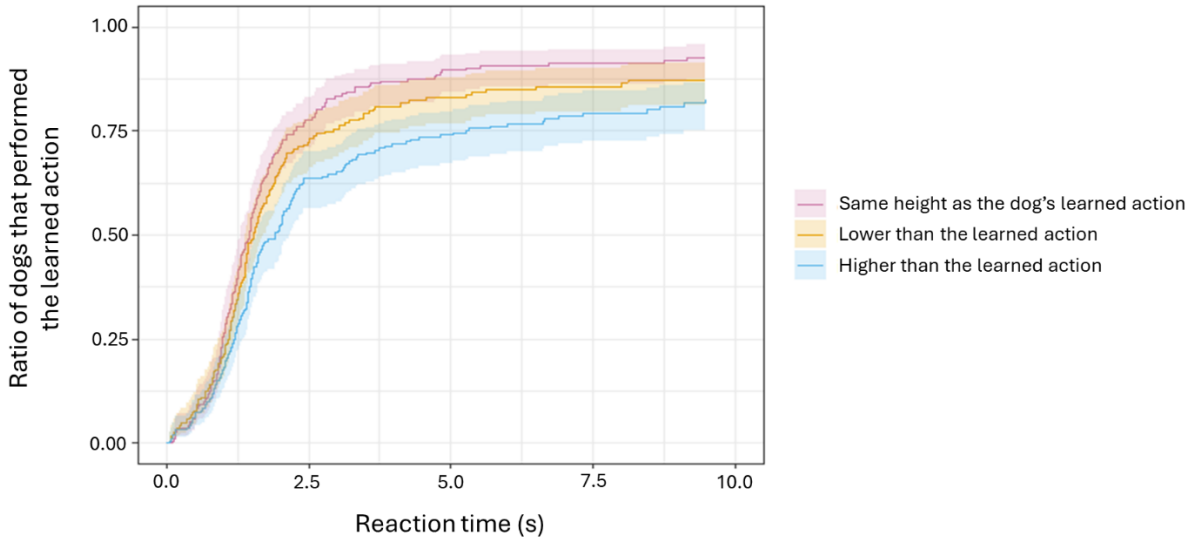
462 Another test of motor interference was conducted immediately after the training. Dogs
463 performed the learned action in 1004 out of 1152 trials during this test (i.e., in 87% of all trials;
464 for a full description of dogs' responses, see Table S5 in the Supplementary File). The presence
465 of human action affected the dogs' reaction times during this second test (full model vs. null
466 model comparison: $\chi^2 = 59.50$, df = 1, $P < 0.0001$; full LMM results: effect of human action: χ^2
467 = 59.95, df = 1, $P < 0.0001$; HR = 1.65, 95%CI = [1.45; 1.87], z = 7.74). The CMM did not
468 reveal an effect of dog sex ($\chi^2 = 1.40$, df = 1, P = 0.237; HR =1.22, 95%CI= [0.88; 1.71], z =
469 0.24) and dog age ($\chi^2 = 1.07$, df = 1, P = 0.302; HR = 0.96, 95%CI = [0.89; 1.04], z = 0.30).
470 The dogs' reaction time to perform their action was longer when the human performed an action
471 (n = 496 out of 575, 1812.06 ± 66.84 ms) compared to trials without human action (508 out of
472 577 trials, 1088.12 ± 48.89 ms). The reaction time for the human to perform their action (575
473 trials) was 560.64 ± 9.44 ms. Note that the experimenter forgot to perform their action in one
474 trial, explaining why there was 575 trials with a human action instead of 576.

475 Considering dogs' reaction time for trials with a human action (575, of which the learned action
476 was executed in 496 trials), the variables of interest significantly improved the model compared
477 to the null model (full model vs. null model comparison: $\chi^2 = 23.58$, df = 11, P = 0.014). The
478 CMM revealed a significant effect of height of human action (Table 4), post-hoc tests yielded
479 the following results: same height as the learned action vs higher: ratio ± SE = 1.37 ± 0.16, 95%
480 CI = [1.05; 1.79], z ratio = 2.79, P = 0.014; same height as the learned action vs lower: ratio ±
481 SE = 1.21 ± 0.14, 95% CI = [0.93; 1.58], z ratio = 1.74, P = 0.191; higher vs lower: ratio ± SE
482 = 0.89 ± 0.10, 95% CI = [0.68; 1.16] z ratio = -1.07, P = 0.535. Dogs performed their action
483 quicker when the human action was congruent in terms of height than when it was higher than
484 the learned action (Figure 6).

Fixed effect	HR	z	95% CI	χ^2	P
Training type (incongruent training)	0.88	-0.42	[0.48; 1.62]	0.18	0.675
Height (higher)	0.60	-2.21	[0.38; 0.94]	6.32	0.042
Height (lower)	0.61	-2.09	[0.39; 0.97]		
Human body part (elbow)	0.80	-1.03	[0.52; 1.22]	1.07	0.301

Training type (incongruent training): Height (higher)	1.82	1.87	[0.97; 3.41]	5.63	0.060
Training type (incongruent training): Height (lower)	2.01	2.17	[1.07; 3.77]		
Training type (incongruent training): Human body part (elbow)	1.22	0.63	[0.66; 2.24]	0.39	0.530
Height (higher): Human body part (elbow)	1.14	0.41	[0.61; 2.13]	0.19	0.908
Height (lower): human body part (elbow)	1.11	0.33	[0.59; 2.10]		
Training type (incongruent training): Height (higher): Human body part (elbow)	0.50	-1.54	[0.21; 1.20]	2.46	0.293
Training type (incongruent training): Height (lower): Human body part (elbow)	0.65	-0.97	[0.27; 1.56]		
Dog sex (male)	1.30	1.07	[0.81; 2.09]	1.15	0.284
Dog age	0.96	-0.79	[0.86; 1.07]	0.62	0.432

Table 4. Results of the CMM for dogs' reaction times in trials with a human action during the motor interference test following the training. The predictors were dummy coded, with training type (congruent training), height (same height as the learned action) and human body part (hand) being the reference categories. HR refers to the estimates of the ratio of the hazard rate for the reported level of a predictor versus the reference category of that predictor.



490

491 **Figure 6.** Proportion of dogs performing the learned action according to time during the test of
492 motor interference following the training, for each height of human action. Shading ± 95% CI.

493

494 Regarding dogs' gazing behaviour during trials with a human action (575 trials), the full model
495 of gaze towards the human action significantly differed from the null model (χ^2 = 27.93, df =
496 11, P = 0.003). The full model analysis revealed an interaction between training type and human
497 body part (Table 5). Post-hoc tests showed a significant difference in dogs' gaze behaviour
498 towards hand actions versus elbow actions for dogs that underwent an incongruent training
499 (Figure 7, odds ratio ± SE = 1.63 ± 0.20, 95% CI = [1.19; 2.22], z ratio = 4.04, P = 0.0003). All
500 other pairwise comparisons were not significant (Table S6 in the Supplementary File). The full
501 model of gaze towards the human did not significantly differ from the null model (χ^2 = 6.80, df
502 = 11, P = 0.815). The dogs spent 7.44 ± 0.54 % of trial time gazing at the human.

503

Fixed effect	β	SE	z	95% CI	χ^2	P
Intercept	0.16	0.29	0.53	[-0.41; 0.72]	0.28	0.594
Training type (incongruent training)	0.15	0.31	0.48	[-0.47; 0.77]	0.23	0.633
Height (higher)	-0.30	0.21	-1.50	[-0.71; 0.10]	2.89	0.235
Height (lower)	-0.30	0.21	-1.45	[-0.71; 0.11]		

Human body part (elbow)	-0.07	0.21	-0.33	[-0.48; 0.34]	0.11	0.740
Training type (incongruent training): Height (higher)	0.14	0.29	0.47	[-0.43; 0.70]	0.52	0.772
Training type (incongruent training): Height (lower)	0.20	0.29	0.71	[-0.36; 0.77]		
Training type (incongruent training): Human body part (elbow)	-0.65	0.29	-2.20	[-1.22; -0.07]	4.85	0.028
Height (higher): Human body part (elbow)	-0.16	0.30	-0.53	[-0.74; 0;42]	1.23	0.542
Height (lower): human body part (elbow)	0.17	0.29	0.58	[-0.41; 0.74]		
Training type (incongruent training): Height (higher): Human body part (elbow)	0.39	0.41	0.95	[-0.42; 1.21]	0.96	0.618
Training type (incongruent training): Height (lower): Human body part (elbow)	0.29	0.42	0.69	[-0.53; 1.10]		
Dog sex (male)	-0.12	0.26	-0.48	[-0.63; 0.38]	0.23	0.631
Dog age	-0.09	0.06	-1.60	[-0.21; 0.02]	2.56	0.109

Table 5. Results of the GLMM for dogs' gaze towards human action during the motor interference test following the training. The predictors were dummy coded, with training type (congruent training), height (same height as the learned action) and human body part (hand) being the reference categories. β refers to the difference of the response between the reported level of a predictor and the reference category of that predictor.



Figure 7. Dogs' gaze towards human hand and elbow actions for both experimental groups. *** P<0.001.

Discussion

This is the first study to investigate motor interference in domestic dogs observing human actions. Based on the hypothesis that behavioural copying of dogs upon humans relies on similar cognitive processes as those found in humans (Lamontagne & Gaunet, 2024), we predicted that dog would show longer reaction times to perform a learned paw action when a human simultaneously executed height-incongruent hand actions compared to congruent actions. Elbow actions were included to investigate the link between motor representations and motor interference (Paulus et al., 2011), which has never been studied before in dogs to our knowledge. We expected no motor interference if the human action was performed with the elbow instead of the hand, as motor resonance cannot occur for actions outside the observer's motor repertoire. Our results revealed that human actions disrupted the dogs' execution of their learned action, but not in the way we expected. First, the increased reaction times trials with human actions compared to those without actions confirm the dogs' strong sensitivity to human behaviours, as previously demonstrated in the literature (see Siniscalchi et al., 2018 for a review). When specifically comparing trials involving human actions, we found a trend towards longer reaction times when the human actions were incongruent in terms of height compared to congruent ones, as expected, though this difference was not statistically significant. Additionally, contrary to our expectations, dogs took longer to perform their action when the human used their elbow rather than their hand.

These findings prompt us to reflect on the cognitive processes involved in motor interference when dogs observe human actions. The trend for the effect of height and the significant effect of body part suggest that the dogs did not process the human actions as a whole; instead, it seems that the movement direction (the height to which the human's movement is directed) and the body part (hand or elbow) relied on distinct cognitive processes. This aligns with human studies, which showed that movement type and body part influence motor interference at least partially independently (Cross et al., 2013; Leighton & Heyes, 2010; Roberts et al., 2016). In the next paragraphs, we expand about the potential processes involved.

It is possible that the processing of movement direction relied on motor resonance, as in humans (Brass et al., 2001; Heyes et al., 2005; Obhi & Jeremy Hogeveen, 2010), since dogs are capable of placing their paw at all three heights. Motor interference would then result from movement compatibility, due to the simultaneous activation of the representations of the perceived movement and that of the executed movement (Cracco et al., 2018). However, it is important to note that in humans, spatial compatibility – when a stimulus interferes with the response due to differing relative positions – also affects motor interference (Cooper et al., 2013; Cracco et al., 2018). As the human and the dog actions were in the same vertical plane in our paradigm, we can't rule out the possibility of a spatial compatibility effect, with the height of the human actions interfering to some extent with the dogs' action due to relative positional differences. In any case, our findings suggest that cognitive processes similar to those seen in humans (movement and/or spatial compatibilities) are at play in dogs.

With regards to the processing of human body part, motor resonance could not be at play, since the elbow actions were impossible for dogs, meaning they could not have motor representations for this type of action. Range et al. (2011) also found an effect of body part on dogs' behaviours – the dogs required more trials to reach the criterion performance when a human demonstrated an action using a different body part than the one the dogs had to use. However, a key difference between that study and ours is that in Range et al. (2011), the human actions were within the canine motor repertoire, so the body part effect they found may rely on effector compatibility, due to the activation of the representations of the perceived body part and those of the body part used, as in humans (Biermann-Ruban et al., 2008; Brass et al., 2001). Since the dogs could not have motor representations of the elbow actions, what process was at play in our study? One possibility is social referencing, as the elbow is not a commonly used body part in human actions, and dog exhibit social referencing in unusual situations, by seeking information from humans and adjusting their behaviour to that of humans (Merola et al., 2012). However, social referencing is unlikely in our experiment, as it implies referential looks towards the unusual stimulus, and we found no significant difference in dogs' gaze behaviour towards hand versus

elbow actions during the test of motor interference. Another possibility is a mismatch between dogs' predictions and the action they observed. Dogs indeed have the ability to predict human actions (Kubinyi et al., 2003), and a study showed that using an unfamiliar body part delayed dogs' ability to predict the goal of a human action (Lonardo et al., 2023). The dogs in our study may have predicted hand actions when the experimenter started to move, and the unexpected elbow movement created a mismatch, delaying their response. This kind of mismatch effect has also been observed in humans (Cross et al., 2013).

The significant differences between two heights, along with the absence of body part effect during the test following congruent or incongruent training, supports the cognitive mechanisms we propose: movement compatibility, coupled with spatial compatibility for the movement direction and mismatch in predicting the body part. Although it is only speculative as there was no significant body part effect during the test of motor interference conducted after the visuomotor training, we suggest that the initial mismatch faded, the use of the elbow no longer being unfamiliar after a few exposures. This would align with previous results showing that dog quickly make neuronal associations (Prichard et al., 2018).

In this study, we also examined the effect of visuomotor training on dogs' behavioural response. Based on the ASL model (Heyes, 2016) which posits that motor interference depends on sensorimotor experience, we expected that dogs repeatedly exposed to incongruent human actions would then not display motor interference, unlike dogs repeatedly exposed to congruent human actions. Our findings of the test of motor interference following visuomotor training indicated that all dogs took longer to perform their action when the human action was higher than the learned one, regardless of whether the experimenter used their hand or elbow, and with no significant difference between the two experimental groups, contrary to what was predicted by the ASL model. However, the two experimental groups differed in terms of dogs' visual attention: dogs that underwent incongruent training spent more time gazing at hand actions than elbow actions during the post-training test of motor interference. This suggests that the incongruent training was sufficient to integrate the hand into the dog's behavioural sequence (i.e., associating the sound and the hand with placing the paw on the trestle), even though this was not reflected in their reaction times. It is possible that 12 exposures to the human action were insufficient to affect motor interference, or that $ experience does not impact motor interference at all, although this is unlikely given the results of previous studies showing that training affected dog behavioural response (Range et al., 2011; Marshall-Pescini et al., 2008). The lack of a statistical significance in our results prevents us from drawing further conclusions.

This study presents several limitations. First, the number of repetitions may have been too low to produce a strong effect of height or a clear impact of sensorimotor training. Studies in humans

involve hundreds of trials per participant (Cracco et al., 2018), increasing the number of repetitions would enhance statistical power and potentially yield more pronounced effects. However, this would require extending the number of sessions for dogs to avoid fatigue or loss of interest, raising methodological concerns. Additionally, to reliably compare the dogs' responses and ensure that they were not acting randomly, a success criterion was needed at the end of the learning phase. This required the inclusion of highly trained dogs who could reach this criterion in a few sessions, as highly trained dogs tend to success complex tasks more quickly than untrained dogs (Marshall-Pescini et al., 2016). Moreover, approximately two-thirds of the dogs were shepherd breeds, which is not surprising as herding breeds are more trainable than other breeds (Turcsán et al., 2011). One could argue that these elements might limit generalizability to the broader domestic dog population, but it seems unlikely that imitation relies on different cognitive processes in highly trained dogs and untrained dogs. A previous study indeed showed that all socialized dogs were able to learn a general imitation rule (Fugazza & Miklosi, 2014). It is also important to note that the extensive learning phase in our study may have introduced a strong learning effect that overshadowed the motor interference mechanism, especially since these dogs were accustomed to performing actions on command regardless of surrounding conditions. In addition, our protocol required food rewards at each trial, even after learning, as dogs tend to lose interest after just a few repetitions without food rewards (Fugazza et al., 2023). The presence of food rewards may have influenced dogs' behaviours in our experiment, but these same authors show that action copying in dogs does not depend on food rewards.

Our findings open new avenues for investigating the interspecific motor resonance hypothesis as a foundation for imitation between dogs and humans. Moreover, this study offers a deeper understanding of the cognitive roots of imitation. It demonstrates that distantly related species can share cognitive mechanisms such as sensitivity to actions, movement and spatial compatibility effects, and action prediction. To further investigate these cognitive roots, it would be valuable to study motor interference in other mammalian species, such as non-human primates—where mirror neurons, the neural basis of imitation, were first discovered—or in other species phylogenetically distant to humans but sharing the same environment, like cats or horses.

Conclusion

This study marks the first investigation of motor interference in a non-human species. We found that when humans performed incongruent actions, it interfered with dogs' execution of learned

actions, although we did not find an effect of sensorimotor training on interspecific motor interference. These findings provide valuable insights into canine cognition, particularly extending research on how dogs process human actions (Martinez et al., 2023; Marshall-Pescini et al., 2014; Wallner Werneck Mendes et al., 2024) and revealing that similar processes underly motor interference in humans and in dogs observing human actions. Our study serves as a pedestal to investigate motor interference in dogs, and we recommend future research explore other contexts for measuring it, potentially using actions that naturally engage the dogs without relying on food rewards.

Data Availability statement: Datasets are accessible in the Open Science Framework repository at the following link:

https://osf.io/rszp3/?view_only=e480c5cbf4124e9fb22001c893a5c10b

Conflict of interest: The authors have no relevant conflict of interest to disclose.

Acknowledgements: The authors would like to express their sincere gratitude to the dog owners who volunteered for this study. We also thank Marine Brunel for her advice on dog training, her expertise having greatly contributed to the improvement and standardization of the learning phase, and Julie Morin and Anouk Gence for the behavioural coding.

Funding: This work was supported by the National Association for Research and Technology (ANRT), the association *Agir pour la Vie Animale*, the French National Centre for Scientific Research (CNRS), and Aix-Marseille University.

Author contributions: Angélique Lamontagne: conceptualization, methodology, formal analysis, investigation, data curation, writing original draft, visualization. Thierry Legou: conceptualization, methodology, validation, investigation, writing review and editing. Thierry Bedossa: conceptualization, resources, funding acquisition. Florence Gaunet: conceptualization, methodology, validation, writing review and editing, supervision.

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Supplementary File

Table S1. Dogs' breeds. Prior to the procedure, the dogs were randomly assigned to one of the two experimental groups, by counterbalancing sexes and with no consideration of the dogs' breeds.

Congruent training (*n* = 16)	**Incongruent training (*n* = 16)**
1 Australian kelpie	1 Australian kelpie
3 Australian shepherd	2 Australian shepherd
1 Belgian Shepherd	1 Belgian Shepherd
2 Border collie	1 Border collie
1 Eurasier	1 Cane Corso
1 Labrador	1 Kooikerhondje
2 Mixed	1 Molossoid crossbreed
1 Pointer	1 Miniature American shepherd
1 Pyrenean sheepdog	1 Mixed
1 White Swiss shepherd dog	5 Sheepdog crossbreed
1 Sheepdog crossbreed	1 Shetland sheepdog
1 Staffordshire bull terrier	

Table S2. Dogs' learning progression. The number in each cell represents the step the dog completed at the end of the corresponding learning session.

Learning session / Dog ID	1	2	3	4	5	6
Dog_1	5	7				
Dog_2	3	4	5	5	6	7
Dog_3	3	4	5	6	7	
Dog_4	3	5	5	7		
Dog_5	5	7				
Dog_6	5	5	7			
Dog_7	3	4	5	7		
Dog_8	3	4	5	5	7	
Dog_9	3	5	5	7		
Dog_10	2	4	5	7		
Dog_11	4	5	6	7		
Dog_12	3	5	7			
Dog_13	3	4	7			
Dog_14	3	5	7			
Dog_15	3	5	6	7		
Dog_16	3	4	7			
Dog_17	4	5	5	7		
Dog_18	3	4	7			
Dog_19	4	5	7			
Dog_20	3	5	7			
Dog_21	3	5	7			
Dog_22	3	5	7			
Dog_23	4	7				
Dog_24	2	4	5	7		
Dog_25	4	6	7			
Dog_26	2	4	5	5	6	7
Dog_27	4	5	7			
Dog_28	3	5	6	7		
Dog_29	2	5	5	7		
Dog_30	2	4	5	7		
Dog_31	3	5	7			
Dog_32	3	5	5	7		

Table S3. Dogs' responses during the first test of motor interference. Out of 1152 trials (36 per dog), there were 1008 instances of correct responses (the dogs performing the learned action), 104 instances of incorrect responses (the dogs performing an action that was not the learned action) and 40 trials where the dogs did not perform any action.

Human's action / Dog's response	Same height as the learnt action		Too high relative to the learnt action		Too low relative to the learnt action		No human action
	Hand	Elbow	Hand	Elbow	Hand	Elbow	
Paw on learned bracket	90	86	83	82	83	82	502
Paw on bracket higher than the one learned	1	3	4	8	2	3	9
Paw on bracket lower than the one learned	2	3	5	3	7	8	46
No response	2	5	4	3	3	4	19

Table S4. Dogs' responses during the visuomotor training for each experimental group. Out of 384 trials (12 per dog), there were 332 instances of correct responses (the dogs performing the learned action), 37 instances of incorrect responses (the dogs performing an action that was not the learned action) and 15 trials where the dogs did not perform any action.

Type of training / Dog's response	Congruent training (16 dogs)	Incongruent training (16 dogs)
Paw on learned bracket	169	163
Paw on bracket higher than the one learned	3	8
Paw on bracket lower than the one learned	12	14
No response	8	7

Table S5. Dogs' responses during the second test of motor interference (immediately after the visuomotor training). Out of 1152 trials (36 per dog), there were 1004 instances of correct responses (the dogs performing the learned action), 97 instances of incorrect responses (the dogs performing an action that was not the learned action) and 51 trials where the dogs did not perform any action.

Human's action / Dog's response	Same height as the learnt action		Too high relative to the learnt action		Too low relative to the learnt action		No human action
	Hand	Elbow	Hand	Elbow	Hand	Elbow	
Paw on learned bracket	89	88	78	77	80	84	508
Paw on bracket higher than the one learned	1	4	6	11	2	1	15
Paw on bracket lower than the one learned	3	1	9	2	11	2	29
No response	3	3	3	6	2	10	24

Table S6. Post-hoc tests of the effect of the interaction between training type and human body part on dogs' gaze towards the human action.

Contrasts	Odds ratio	SE	95% CI	Z ratio	P
Congruent training – hand action/ Incongruent training – hand action	0.77	0.21	[0.39; 1.52]	-0.99	0.755
Congruent training – hand action/ Congruent training – elbow action	1.07	0.13	[0.78; 1.45]	0.54	0.950
Congruent training – hand action/ incongruent training – elbow action	1.25	0.34	[0.63; 2.49]	0.84	0.838
Incongruent training – hand action/ congruent training – elbow action	1.39	0.37	[0.70; 2.76]	1.23	0.607
Incongruent training – hand action/ incongruent training – elbow action	1.63	0.20	[1.19; 2.22]	4.04	0.0003
Congruent training – elbow action/ incongruent training – elbow action	1.17	0.32	[0.59; 2.34]	0.59	0.935

CMMs of dogs' reaction time to place their paw elsewhere than on the learned bracket

Test of motor interference

The presence of a human action delayed the dogs' reaction time to place their paw elsewhere than on the learned bracket (full-null model comparison: $\chi^2 = 18.86$, df = 1, $P < 0.0001$). Full CMM results are presented below:

Fixed effect	HR	z	95% CI	χ^2	P
Action (no human action)	2.43	4.36	[1.63; 3.63]	18.99	<0.0001
Dog sex (male)	1.07	0.22	[0.58; 1.96]	0.05	0.826
Dog age	1.11	1.55	[0.97; 1.27]	2.41	0.121

Considering only trials with a human action, the full-null model comparison was not significant ($\chi^2 = 3.72$, df = 5, $P = 0.591$), meaning the variables of interest did not affect the dogs' reaction time to place their paw elsewhere than in the learned bracket.

Test of the effect of visuomotor training on dog's behavioural response

The presence of a human action tended to affect the dogs' reaction time to place their paw elsewhere than on the learned bracket (full-null model comparison: $\chi^2 = 2.89$, df = 1, $P = 0.089$).

Considering only trials with a human action, the full-null model comparison was significant ($\chi^2 = 28.11$, df = 11, $P = 0.003$). Full CMM results are presented below:

Fixed effect	HR	z	95% CI	χ^2	P
Training type (incongruent training)	0.16	-1.37	[0.01; 2.16]	1.46	0.227
Height (higher)	2.66	1.46	[0.72; 9.82]	5.42	0.067
Height (lower)	2.26	1.20	[0.59; 8.64]		
Human body part (elbow)	0.23	-1.26	[0.02; 2.27]	2.61	0.106
Training type (incongruent training): Height (higher)	2.62	0.75	[0.21; 33.02]	0.40	0.819
Training type (incongruent training): Height (lower)	2.31	0.63	[0.17; 31.16]		

Training type (incongruent training): Human body part (elbow)	19.47	1.82	[0.80; 472.79]	0.57	0.449
Height (higher) : Human body part (elbow)	2.87	0.84	[0.24; 33.67]	0.76	0.685
Height (lower): human body part (elbow)	1.35	0.22	[0.10; 18.94]		
Training type (incongruent training): Height (higher): Human body part (elbow)	0.05	-1.66	[0.01; 1.72]	2.76	0.252
Training type (incongruent training): Height (lower): Human body part (elbow)	0.00	0.00	[0; inf]		
Dog sex (male)	0.81	-0.33	[0.22; 2.94]	0.11	0.744
Dog age	1.21	1.27	[0.90; 1.62]	1.61	0.204

6. Discussion générale

6.1. Synthèse des résultats

Après une revue approfondie de la littérature sur les modulateurs sociaux potentiels de la synchronisation comportementale entre le chien et l'humain, cinq études expérimentales ont été menées pour explorer l'influence de certains de ces modulateurs.

Nous avons en premier lieu étudié l'effet du comportement d'une personne inconnue sur la synchronisation locomotrice du chien envers cette personne (Chapitre 2). Nous avons utilisé un protocole de marche en ligne droite de 45 secondes, pour comparer dans une première étude la synchronisation des chiens sur la personne selon qu'elle s'était ou non synchronisée sur eux, et dans une seconde étude selon qu'elle s'était ou non synchronisée sur les propriétaires. Les résultats montrent que le fait de se synchroniser avec le chien ou le propriétaire influence la synchronisation locomotrice du chien. Concrètement, les chiens sur lesquels la personne avait synchronisé sa locomotion étaient ensuite plus proches d'elle d'environ 5 mètres et montraient un écart de vitesse plus faible d'environ 0,5 m/s au début de la marche, par rapport aux chiens sur lesquels la personne avait désynchronisé sa locomotion. De façon similaire, les chiens pour lesquels la personne avait synchronisé sa locomotion sur celle du propriétaire étaient plus proches d'elle d'environ 7 mètres, montraient un écart de vitesse plus faible d'environ 0,7 m/s au début de la marche, et 3 fois plus de chiens de ce groupe ajustaient leur vitesse au moment où la personne changeait de vitesse de marche, par rapport aux chiens pour lesquels la personne avait désynchronisé sa locomotion sur celle du propriétaire. Toutefois, cet effet était temporaire : tous les chiens avaient tendance à revenir vers leur propriétaire, cet effet d'attraction étant retardé d'environ 20 secondes lorsque la personne s'était synchronisée avec eux.

Nous avons également examiné l'effet du nombre de personnes entourant le propriétaire sur la synchronisation locomotrice des chiens (Chapitre 3). En utilisant le même protocole de marche en ligne droite, nous avons montré que les chiens ajustaient leur locomotion sur celle de leur propriétaire, sans effet du nombre de personnes autour. En effet, que les propriétaires soient seuls, avec 2 ou 4 autres personnes, les chiens restaient à environ 5 mètres de leur propriétaire, avec un écart de vitesse d'approximativement 0.5m/s et ils mettaient en moyenne 2 secondes pour adapter leur vitesse quand les humains changeaient de vitesse. En revanche, lorsque le groupe se séparait, le propriétaire d'un côté et les 4 autres personnes de l'autre, 75% des chiens ont suivi le groupe, et ce pendant environ 20 secondes, tous ces chiens sauf un ont ensuite rejoint leur propriétaire.

La dernière étude utilisant le contexte de la marche visait à comparer la synchronisation locomotrice des chiens avec un congénère familier et avec un humain familier (Chapitre 4). Cette étude a été menée dans un espace extérieur clos, en observant les déplacements spontanés car il aurait été difficile d'apprendre au congénère familier à

suivre un parcours prédéfini sans que cela affecte le comportement des chiens. Néanmoins, l'humain familier avait reçu des consignes pour que les conditions soient le plus comparables possible. Les résultats montrent une synchronisation de localisation plus forte entre congénères, la distance moyenne étant d'environ 2m plus faible qu'avec l'humain familier, ainsi qu'une synchronisation de vitesse plus élevée mais seulement pour les chiens ne vivant pas avec un autre chien : l'écart de vitesse avec le congénère était en moyenne 0,2 m/s inférieur à l'écart avec l'humain familier.

L'investigation de la modulation de la synchronisation interspécifique soulève la question des processus cognitifs qui la sous-tendent. Nous avions proposé l'hypothèse de la résonance motrice interspécifique, néanmoins les études sur la modulation sociale ne permettent pas d'y apporter avec certitude des éléments de réponse. Dans ce contexte, nous avons mis en œuvre une expérience pour fournir des preuves en faveur ou en défaveur de cette hypothèse. L'étude sur l'interférence motrice (Chapitre 5) avait ainsi pour objectif de mettre en évidence une manifestation comportementale de la résonance motrice lorsque les chiens observent des actions humaines. Après une phase d'apprentissage d'une action spécifique, les résultats de l'étude indiquent une tendance à un allongement des temps de réaction des chiens pour exécuter l'action apprise lorsqu'il y avait simultanément une action humaine incongruente en termes de hauteur, par rapport à une action congruente et un allongement significatif de ces temps de réaction lorsque l'action humaine était effectuée avec une autre partie du corps que la main, le coude en l'occurrence. La moitié des chiens avait ensuite été exposée à un entraînement sensorimoteur congruent, l'autre moitié à un entraînement incongruent, mais nous n'avons pas observé de différence significative entre ces deux groupes sur les temps de réaction des chiens pendant le test suivant l'entraînement. Quel que soit le groupe expérimental, les temps de réaction était significativement allongés si l'action humaine était trop haute plutôt qu'à la hauteur apprise par les chiens, et l'effet de la partie du corps n'était plus présent. En revanche, les deux groupes différaient dans leur attention visuelle : les chiens qui avaient eu l'entraînement incongruent passaient plus de temps à regarder les actions de la main que celles du coude.

En résumé, nos études ont mis en évidence l'effet de certains modulateurs sociaux : le comportement d'une personne inconnue vis-a-vis du chien ou de son propriétaire, le nombre de personnes et le type d'agent social. Bien que cela n'ait pas été notre objectif initial, nos résultats soulignent l'importance de la présence du propriétaire et son effet d'attraction. En effet, même si les chiens étaient en train de marcher avec une personne inconnue, ou en train de suivre un groupe familier de 4 personnes, ils finissaient par revenir vers leurs propriétaires. Nos résultats auraient certainement été différents si les propriétaires avaient été absents dans nos protocoles, comme observé lors des pré-tests de l'étude du Chapitre 4. Finalement, dans l'ensemble, les recherches menées au cours de la thèse fournissent des informations modulant l'implication des bases neurocognitives de la synchronisation comportementale du chien sur l'humain.

6.2. Implications théoriques

6.2.1. Contributions au regard de la théorie de la résonance motrice interspécifique

La synchronisation comportementale entre le chien et l'humain est désormais largement documentée. L'objectif principal de cette thèse était d'identifier certains facteurs sociaux qui la modulent. Cette investigation permet de mieux comprendre ses bases cognitives, notamment au regard de la théorie de résonance motrice interspécifique que nous avons présentée. Cette thèse, par son approche comportementale, ne rend pas possible la validation ou le rejet de cette théorie. Néanmoins, nous avons obtenu des résultats qui la soutiennent. Ces observations m'amènent à proposer un modèle en deux étapes, inspiré de celui existant chez l'humain, pour expliquer la synchronisation comportementale interspécifique sur la base de la résonance motrice.

6.2.1.1. Les preuves soutenant que la synchronisation comportementale du chien sur l'humain est fondée sur les représentations sensorimotrices

Comme indiqué dans l'introduction générale, il est établi chez l'humain que la perception d'une action active les représentations sensorimotrices associées à cette action chez l'observateur, ou « résonne » avec ces représentations motrices, c'est pourquoi on parle de résonance motrice. Ceci rend l'observateur plus enclin à exécuter l'action perçue (pour des revues récentes, voir Bonini et al., 2022; Lamontagne & Gaunet, 2023; Rizzolatti & Sinigaglia, 2016). La résonance motrice entraîne alors une réponse imitative automatique, conduisant à une propagation du comportement entre individus.

Nous avons proposé l'hypothèse selon laquelle un mécanisme similaire s'applique aux interactions chien-humain. Plus précisément, la perception d'une action humaine par le chien activerait les représentations sensorimotrices associées à cette action chez le chien, par résonance motrice interspécifique. Cela entraînerait alors une réponse imitative automatique chez le chien, et une propagation comportementale de l'humain vers le chien, menant à la synchronisation comportementale interspécifique.

Les résultats des études menées au cours de la thèse mettent effectivement en évidence une propagation comportementale, locomotrice en l'occurrence, de l'humain vers le chien. En effet, nos protocoles expérimentaux de marche en ligne droite (Chapitres 2 et 3) ont permis de constater que lorsque les humains se mettaient en mouvement, au début de la marche, les chiens se mettaient également en mouvement. De plus, lorsque c'était une personne non familière qui marchait (Chapitre 2), les chiens ne maintenaient pas leur synchronisation si celle-ci s'était au préalable désynchronisée des chiens ou de leurs propriétaires ; en revanche ils se synchronisaient temporairement sur la personne si elle s'était alignée au préalable sur les chiens ou leurs propriétaires. Je discuterai cet aspect temporaire de la synchronisation de la marche du chien dans la section suivante. Dans

l'étude impliquant les propriétaires, seuls ou en groupe (Chapitre 3), les chiens se synchronisaient sur les humains tout au long de la marche en ligne droite. Cela a donné l'occasion de mettre en évidence, une fois de plus, une propagation systématique du comportement de marche de l'humain vers le chien, lorsque les humains passaient de la condition statique à une condition de marche.

Cette propagation comportementale de l'humain vers le chien implique-t-elle une activation, chez ce dernier, des représentations sensorimotrices du comportement perçu ? L'étude présentée au Chapitre 5, qui explore l'interférence motrice chez le chien de compagnie, apporte des éléments de réponse à cette question. Inspirée des protocoles utilisés chez l'humain, cette étude a mis en évidence qu'une action humaine incongruente interférait avec l'exécution d'une action chez les chiens. Ce résultat est compatible avec l'hypothèse de la résonance motrice interspécifique, qui impliquerait donc l'activation des représentations sensorimotrices du mouvement humain observé, incitant une réponse imitative automatique chez le chien. Néanmoins, cette étude comportementale devra être corrélée à des données neuronales pour confirmer la présence de telles représentations, ou du moins de structures neuronales activées à la fois lors de la perception et de l'exécution des actions par le chien, avec la NIRS par exemple. Les études en neuroimagerie, notamment en IRMf, qui émergent ces dernières années, ont révélé des zones cérébrales actives lors de la perception d'actions par le chien (Boch et al., 2023; Karl et al., 2021; Phillips et al., 2022). Ces études, réalisées avec des chiens de compagnie entraînés à rester immobiles sans anesthésie, utilisent du matériel identique à celui employé chez l'humain. Cette recherche a ainsi mis en lumière le rôle prépondérant du lobe temporal dans la perception des signaux sociaux visuels, ce qui inclue la perception d'actions effectuées par des congénères ou des humains. Les compétences sociocognitives plus complexes, comme l'imitation, n'ont pas encore fait l'objet d'études neurologiques, mais l'identification des régions cérébrales impliquées dans la perception des signaux sociaux ouvrent la voie à de futures recherches. Cela permettra de relier les données neuronales et comportementales et de vérifier si des processus cognitifs similaires à ceux observés chez l'humain sont effectivement présents chez le chien. Je précise toutefois qu'étant donné les différences structurelles entre les cerveaux des canidés et des primates (Boch et al., 2024), l'objectif ne serait pas d'identifier des structures cérébrales homologues, mais plutôt d'adapter les protocoles utilisés chez les primates humains et non-humains pour identifier chez le chien des structures impliquées à la fois dans la perception et l'expérience motrice individuelle d'un comportement.

Comment ces représentations sensorimotrices seraient-elles formées ? Selon le modèle ASL, les neurones miroirs sont construits par le biais de l'apprentissage associatif au cours des interactions sociales. Initialement, les neurones sensoriels, qui réagissent aux propriétés visuelles d'un comportement, ne sont que faiblement connectés, voire pas du tout, aux neurones moteurs (Catmur et al., 2016). Au cours du développement, les interactions sociales fournissent aux individus une expérience sensorimotrice corrélée, lorsqu'ils effectuent un comportement observé, ou qu'ils observent d'autres individus effectuer le même comportement qu'eux (Essler et al., 2023; Giudice et al., 2009; Hunnius & Bekkering, 2014). Les connexions entre les neurones sensoriels et moteurs sont ainsi renforcées s'ils sont activés à peu près en même temps et si l'activation des uns prédit l'activation des autres (Cooper et al., 2013). De cette façon, par apprentissage associatif, les neurones moteurs, initialement activés uniquement lors de l'exécution de l'action,

finissent par décharger également lors de l'observation d'une action similaire (Catmur et al., 2016; Heyes, 2010).

Selon le modèle ASL, le développement des neurones miroirs ne nécessite pas de mécanisme cognitif spécialisé ou complexe, il suffit d'un traitement visuel et moteur des actions, ainsi que d'une capacité d'apprentissage associatif (Heyes, 2016). Comme les chiens de compagnie baignent dans l'environnement humain dès leurs premiers jours de vie, il est tout à fait plausible que des connexions entre les représentations sensorielles et motrices de certains comportements se forment, que ces derniers soient effectués par des congénères ou des humains (Range et al., 2011). Pour la marche par exemple, qui est le modèle utilisé dans nos études, il est évident que les chiens ont l'expérience simultanée d'observer la marche des humains pendant qu'ils marchent eux-mêmes. Il est donc possible que les neurones moteurs associés à la marche chez le chien soient connectés aux neurones sensoriels réagissant à la perception de la marche humaine. De cette façon, percevoir un humain marcher activerait automatiquement les neurones moteurs associés à la marche chez le chien.

6.2.1.2. Les preuves en faveur d'une réponse imitative flexible et modulée socialement chez le chien par l'humain ou le chien

Nous avons précédemment décrit comment chez l'humain, la perception d'une action entraine une réponse imitative automatique par résonance motrice. Cette réponse est flexible, elle dépend notamment du nombre d'agents perçus. En effet, les actions de plusieurs agents peuvent être représentées simultanément dans le cortex moteur de l'observateur et plus le nombre d'individus réalisant une action est élevé, plus la résonance motrice et, par conséquent, la réponse imitative automatique, sont fortes (Cracco et al., 2015, 2016, 2019; Cracco & Brass, 2018). De plus, selon le modèle ASL, la résonance motrice repose sur des connexions entre les représentations sensorielles et motrices d'un comportement, qui sont formées et renforcées par l'expérience. Ces connexions sont donc flexibles, en témoigne le fait qu'un entraînement sensorimoteur incongruent peut créer de nouvelles connexions, diminuant voire abolissant la réponse imitative automatique (voir, entre autres, Catmur & Heyes, 2019; Cook et al., 2012; Roberts et al., 2016).

Par ailleurs, il est proposé que cette réponse automatique, issue d'un traitement bottom-up, est ensuite modulée par des processus top-down intervenant en quelques centaines de millisecondes, qui la renforcent ou l'inhibent (Cracco et al., 2022; Jenkins, 2019; Ubaldi et al., 2015). La réponse comportementale finale de l'observateur dépend donc de cette modulation, qui est fonction de facteurs liés à l'observateur, à la personne observée, à leur relation et au contexte social, voire spatial, de l'interaction (Kemmerer, 2021; Wang & Hamilton, 2012). Ainsi, dans certains contextes, la réponse automatique est renforcée, donnant lieu à une réponse comportementale finale imitative, observable par exemple lorsque les agents en interaction sont familiers ou attentifs l'un à l'autre. Dans d'autres contextes, la réponse automatique est inhibée, par conséquent même si l'on peut la détecter, dans les paradigmes d'interférence motrice notamment, la réponse finale de

l'observateur ne sera pas de copier l'action observée. Il est important de noter que cette modulation n'est pas rigide. Par exemple, ce n'est pas parce que deux agents familiers interagissent qu'ils vont forcément s'imiter. Toujours en suivant l'idée que des processus cognitifs similaires à ceux de l'humain existent chez le chien, voyons s'il est possible d'envisager d'une part une flexibilité de l'activation des représentations sensorimotrices et d'autre part une modulation top-down de la réponse automatique chez ce canidé.

Commençons par discuter des propriétés d'activation des représentations sensorimotrices chez le chien. D'abord, l'étude présentée au Chapitre 3, qui examine l'effet du nombre d'humains sur la synchronisation des chiens, montre que ces derniers ont été entrainés par les 4 personnes, et non pas par leur propriétaire, lors de la phase de séparation de groupe. Cet entraînement locomoteur pourrait être le reflet d'une plus forte résonance motrice du fait de la présence de plusieurs humains, par rapport à l'humain seul, à l'instar de ce que l'on observe chez l'humain. D'autre part, les études portant sur l'effet du profil locomoteur sur la synchronisation locomotrice du chien sur l'humain sont également compatibles avec une flexibilité des connexions entre les représentations sensorielles et motrices. En effet, les chiens synchronisent moins leur locomotion avec celle d'un enfant de la famille qu'avec celle de leur propriétaire adulte (Wanser et al., 2021). Etant donné que les chiens ont généralement plus d'expérience de marche avec les humains adultes, et que les enfants ont une locomotion immature par rapport à celle des adultes, il est possible que les représentations motrices de la marche chez le chien soient davantage associées aux représentations sensorielles de la marche d'un humain adulte qu'à celles de la marche d'un enfant. Également, l'étude présentée au Chapitre 4 indique une synchronisation de localisation des chiens plus étroite avec un congénère familier qu'avec un humain familier, et un ajustement de vitesse plus fort avec le congénère pour les chiens qui ne vivaient pas quotidiennement avec un autre chien. Nous pouvons suggérer que cette synchronisation plus marquée en intraspécifique qu'en interspécifique est le résultat de plus fortes associations entre les représentations sensorielles et motrices de la marche pour des individus de la même espèce, d'autant plus que le chien et l'humain ont des schémas locomoteurs différents (quadrupédie vs bipédie). Visiblement, le fait de vivre avec un congénère a un effet sur la synchronisation d'activité. Ces chiens sont davantage témoins d'interactions entre congénères et humains par rapport aux chiens qui vivent sans autre canidé. Peut-être que ces expériences d'observations renforcent les associations entre les représentations sensorielles de la marche humaine et les représentations motrices de la marche chez le chien. Cette hypothèse est soutenue par le fait que selon l'ASL, les connexions sensorimotrices peuvent se former par l'observation d'individus effectuant la même action que soi, par l'exécution d'une action observée et par l'observation de tiers réalisant des comportements synchronisés (Catmur et al., 2016). L'expérience de vie affecterait donc les connexions entre les représentations sensorielles et motrices chez le chien. Bien sûr, la synchronisation plus marquée entre congénères pourrait être simplement liée à des facteurs physiques : le traitement d'un profil locomoteur identique au sien étant connu, il est plus facile de s'ajuster à celui-ci qu'à un profil locomoteur différent, dans le même esprit que la synchronisation locomotrice chez l'humain est atteinte plus rapidement lorsque les individus ont des longueurs de jambes et des cadences de pas similaires (Nessler et al., 2013). Enfin, dans l'étude présentée au Chapitre 5, nous avons examiné l'effet de l'entraînement sensorimoteur sur l'interférence motrice, dans le but de

déterminer si cela affecte la réponse automatique, comme chez l'humain. Nos résultats n'ont pas révélé d'effet significatif, ce qui semble contredire les prédictions du modèle ASL. Toutefois, cela ne signifie pas que l'entraînement sensorimoteur n'a aucun impact, surtout qu'une étude antérieure a mis en évidence un effet de l'entraînement sur la réponse comportementale des chiens (Range et al., 2011). L'absence d'effet dans notre étude pourrait être le résultat d'un nombre de répétitions trop faible pendant l'entraînement par exemple. De futures études sont de ce fait nécessaires pour clarifier cet aspect.

Concernant la modulation de la réponse automatique par des processus top-down, les effets des modulateurs sociaux que nous avons identifiés dans cette thèse sont compatibles avec cette idée. On peut en effet considérer que certains facteurs sociaux, comme le *niveau de familiarité* ou la *présence d'un groupe*, renforcent la réponse imitative automatique, menant à la synchronisation comportementale du chien sur l'humain. La modulation par le niveau de familiarité est particulièrement marquée lorsque le propriétaire est présent, puisque c'est l'humain ayant le plus haut degré de familiarité avec le chien. La présence d'un groupe d'humains peut affecter non seulement l'activation des représentations sensorimotrices, comme indiqué plus haut, mais peut également moduler la réponse imitative automatique, par effet de conformisme par exemple : la réponse automatique est renforcée car elle correspond au comportement produit par la majorité (Claidière & Whiten, 2012). Dans l'étude présentée au Chapitre 3, le fait que les chiens aient suivi le groupe, puis qu'ils aient rejoint le propriétaire après une vingtaine de secondes indique que cette modulation n'est pas rigide. Pendant la marche en ligne droite, nous n'avions pas obtenu de différence entre les deux groupes expérimentaux (chiens avec leur propriétaire seul et chiens avec leur propriétaire et 4 autres personnes). L'effet d'affiliation serait donc plus fort que l'effet de groupe quand les deux modulateurs sont présents en même temps, et l'effet de groupe serait plus fort que l'effet d'affiliation quand les deux modulateurs sont mis en opposition, mais seulement temporairement, c'est à dire tant que le propriétaire n'est pas trop loin et/ou éloigné depuis trop longtemps. On retrouve également une modulation de la réponse comportementale des chiens dans le Chapitre 2. En effet, les études présentées dans ce chapitre révèlent que les chiens ne se synchronisent habituellement pas avec une personne non familière, mais le font temporairement si cette personne a eu un comportement spécifique envers eux ou leurs propriétaires. Ces éléments sont donc cohérents avec l'idée d'une modulation de la réponse imitative chez le chien en fonction de certains facteurs et du contexte social.

6.2.1.3. Bilan : un modèle de synchronisation comportementale du chien sur l'humain résultant d'un processus en deux étapes

Nous avons exposé les éléments en faveur de l'hypothèse de la résonance motrice interspécifique et des processus cognitifs associés. Chez l'humain, un modèle en deux étapes a été proposé : la perception d'une action déclenche d'abord une réponse miroir, puis des processus stratégiques top-down renforcent ou inhibent cette réponse initiale (Cracco et al., 2022 ; Jenkins, 2019 ; Ubaldi et al., 2015). En m'appuyant sur ce qui se produit chez l'humain, je propose un modèle similaire appliqué au chien percevant l'humain, en l'illustrant avec l'exemple de la marche (Figure 6). D'après ce modèle, lorsqu'un chien, immobile, perçoit un humain en train de marcher, cela active chez le chien les représentations sensorimotrices associées à la marche ; l'association entre les représentations sensorielles de la marche humaine et les représentations motrices de la marche chez le chien étant formées au cours de la vie du chien par l'expérience répétée de marcher avec des humains. Par résonance motrice, une réponse automatique imitative est ainsi générée, et se traduit par une mise en mouvement du chien. Cette réponse est d'autant plus forte que le nombre d'humains augmente, et les associations sensorimotrices peuvent être modifiées selon l'expérience de vie des chiens. Cette réponse initiale, qui résulte d'un processus bottom-up, est ensuite modulée par des processus top-down, c'est donc à ce stade qu'interviennent les modulateurs sociaux, tels que la familiarité, l'effet de groupe, l'état attentionnel, etc. (Lamontagne & Gaunet, 2023), qui influencent la réponse comportementale finale du chien.

Je propose ce modèle comme base neurocognitive possible pour expliquer la synchronisation comportementale interspécifique, mais des études neurophysiologiques sont nécessaires pour la valider, en identifiant par exemple des neurones miroirs chez le chien. Si de tels neurones venaient à être découverts, la question resterait de savoir s'ils jouent un rôle de bas niveau, comme la sélection et l'identification d'actions, ou s'ils sont également impliqués dans des fonctions de plus haut niveau, telles que la « compréhension » des actions, c'est-à-dire la détection et l'identification de leur but et de l'intention affiliative ou agonistique. Le débat sur la fonction des neurones miroirs reste d'ailleurs ouvert chez l'humain, où la fonction de bas niveau est largement acceptée, mais celle de haut niveau reste controversée malgré des décennies de recherche (Heyes & Catmur, 2022).

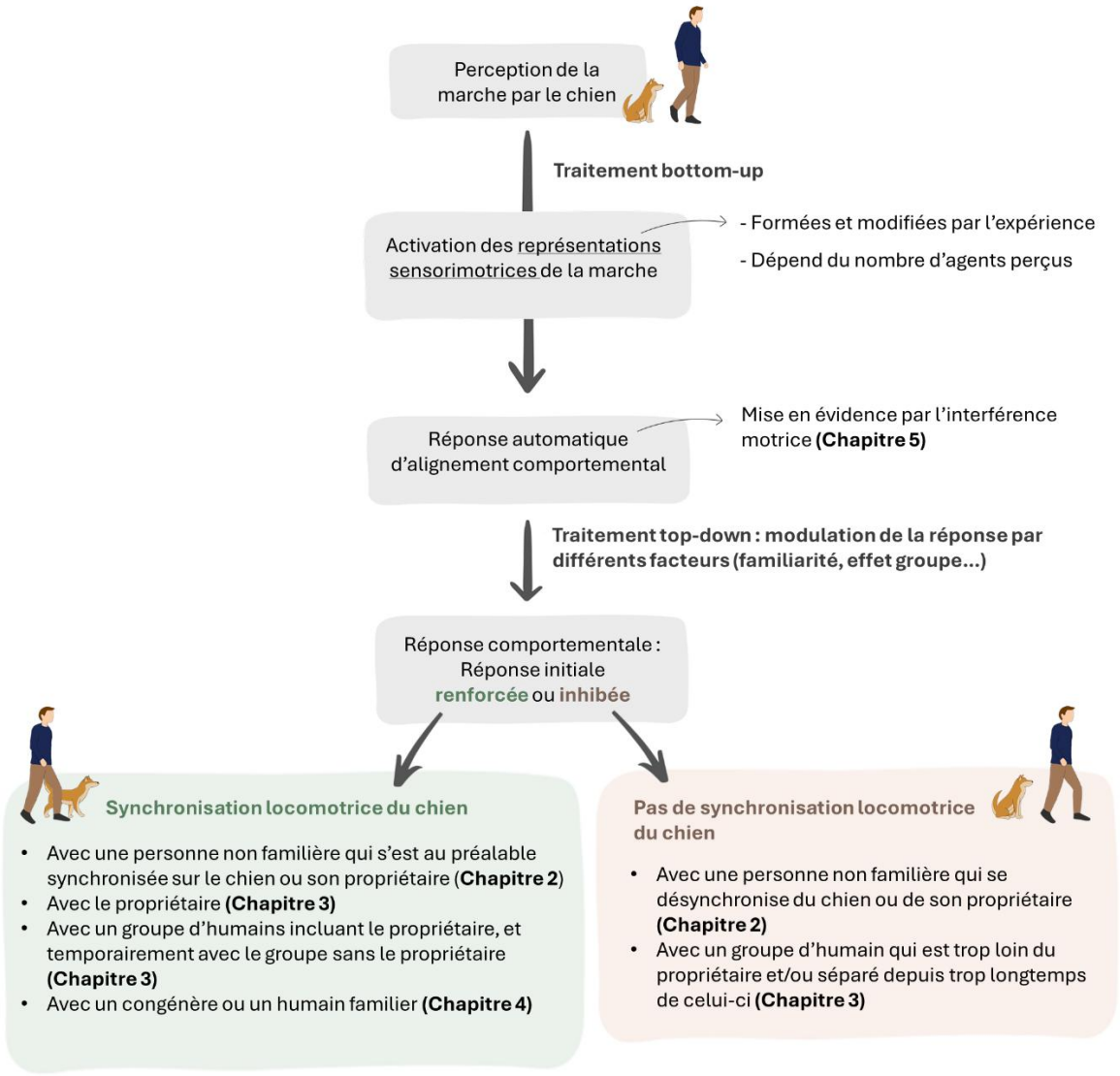


Figure 6. Schéma bilan illustrant le modèle en deux étapes impliquant la résonance motrice interspécifique (processus bottom-up) et une modulation top-down de la réponse automatique.

6.2.2. D'autres processus cognitifs peuvent être impliqués dans la synchronisation comportementale du chien sur l'humain

La thèse apporte des résultats qui étayent l'hypothèse de la résonance motrice interspécifique mais il y a probablement d'autres mécanismes en jeu. La sélection d'une réponse comportementale ne repose certainement pas que sur le système miroir. Dans cette section, je décris les processus cognitifs autres que la résonance motrice qui peuvent être impliqués dans la copie de comportement du chien sur l'humain.

6.2.2.1. L'influence sociale exercée par le propriétaire

Les propriétaires ont un rôle particulier pour les chiens. Ils sont leurs partenaires sociaux préférés (Topál et al., 2009), et ont une fonction de leader, notamment en prenant des décisions quotidiennes concernant les activités partagées avec leurs chiens, comme l'itinéraire ou la durée des promenades. Ils exercent un effet sécurisant pour les chiens, au même titre que celui des mères sur leurs bébés (Cimarelli et al., 2016; Gácsi et al., 2013). Cet effet sécurisant peut expliquer pourquoi lors des promenades, même si les chiens s'éloignent pour explorer, ils reviennent ensuite systématiquement vers leurs propriétaires (Ákos et al., 2014), c'est l'effet « laisse invisible » que le propriétaire exerce sur le chien, à l'instar d'une mère pour son jeune enfant. Un effet comparable a été observé dans les études de la thèse, notamment dans celles impliquant la marche avec une personne non familière (Chapitre 2), où les chiens finissaient tous par s'éloigner en direction de leur propriétaire pendant la marche en ligne droite, la moitié des chiens les ayant même rejoints avant la fin de la marche.

Le comportement des chiens est ainsi fortement influencé par la présence de leur propriétaire. L'influence sociale du propriétaire peut se manifester sous différentes formes, telles que le renforcement local, le renforcement de stimulus ou la facilitation sociale (Mersmann et al., 2011). Par exemple, le comportement du propriétaire envers un objet (renforcement de stimulus) ou le lieu où il se déroule (renforcement local) attire l'attention du chien vers cet objet ou cet endroit précis. De plus, par facilitation sociale, le fait d'observer le propriétaire réaliser une action déjà présente dans le répertoire comportemental du chien augmente la probabilité que celui-ci reproduise ce comportement (Kubinyi et al., 2009; Mersmann et al., 2011). Les chiens se comportent ainsi différemment en présence ou en l'absence de leurs propriétaires. Par exemple, les chiens manifestent davantage de comportements d'exploration et de jeu (Mariti et al., 2013; Prato-Previde et al., 2003) et ont un taux de réussite plus élevé dans une tâche de résolution de problèmes (Horn et al., 2013), en présence de leur propriétaire qu'en présence d'une personne inconnue. Cela explique d'ailleurs pourquoi la présence des propriétaires était nécessaire dans le protocole de l'étude qui comparait la synchronisation locomotrice intraspécifique et interspécifique (Chapitre 4).

Les propriétaires sont même une référence sociale pour les chiens. En effet, face à des situations nouvelles ou étranges, telles qu'une nouvelle personne (Duranton et al., 2016;

Salamon et al., 2020) ou un objet inconnu (Merola et al., 2012a, 2012b), les chiens alternent leur regard entre le nouveau stimulus et leur propriétaire, et adaptent leur réponse comportementale en fonction de celle de leur propriétaire. Ce processus, appelé référencement social, a été initialement étudié chez les bébés humains envers leur mère (Stenberg & Hagekull, 1997) et a été également démontré chez les chiens adultes envers leur propriétaire, mais aussi chez les chiots de 2 mois (Fugazza et al., 2018a). L'ajustement comportemental ne se produit pas en revanche si l'humain informateur est une personne non familière (Merola et al., 2012a; Yong & Ruffman, 2015), ou le soigneur attitré dans le cas des chiens de refuge (Duranton et al., 2017a). Cela suggère que les signaux des propriétaires, mais pas ceux des personnes inconnues, sont des informations pertinentes pour les chiens, et qu'une privation sociale impacte le référencement social. Puisque les chiens n'ont pas d'expérience antérieure lorsqu'ils sont face à de nouvelles situations, se référer au propriétaire est avantageux, cela favorise une réaction rapide et appropriée tout en évitant les risques d'un apprentissage par essais et erreurs (Fugazza et al., 2018). De plus, les informations acquises par référencement social influencent le comportement des chiens lorsqu'ils sont ensuite confrontés, seuls cette fois, à une situation similaire (Fugazza et al., 2018). Le référencement social permet donc un apprentissage social rapide (Salamon et al., 2020), sans qu'il y ait nécessairement des correspondances sensorimotrices préexistantes chez le chien.

Au niveau physiologique, plusieurs études ont mis en évidence une corrélation entre les interactions sociales au sein des dyades chien-propriétaire, par la caresse ou le jeu par exemple, et leurs niveaux d'ocytocine, une hormone produite par l'hypothalamus et associée à des états émotionnels positifs (Handlin et al., 2011; Hritcu et al., 2019; Nagasawa et al., 2009, 2015). Par exemple, Nagasawa et al. (2009, 2015) ont montré une augmentation des niveaux d'ocytocine dans l'urine des chiens et des propriétaires après une interaction sociale positive, entrainant en retour une augmentation de l'activité de regard des chiens envers leur propriétaire. Toutefois, certaines études n'ont pas observé de tels effets (Marshall-Pescini et al., 2019; Powell et al., 2019; Romero et al., 2014). En outre, d'autres publications indiquent une augmentation des niveaux d'ocytocine à la suite d'interactions entre des chiens et des personnes familières (MacLean et al., 2017; Mitsui et al., 2011). L'ocytocine semble donc avoir un rôle dans le comportement des chiens envers leurs propriétaires, mais ce n'est peut-être pas spécifique à cette dyade.

Enfin, des recherches récentes combinant des données de neuroimagerie fonctionnelle (IRMf) et comportementales ont révélé des preuves convergentes que les chiens réagissent différemment à leur humain référent qu'à d'autres agents humains. En effet, la perception du propriétaire (Karl et al., 2020, 2021) ou de l'entraineur pour les chiens de travail (Thompkins et al., 2021), active chez le chien des structures limbiques associées au traitement des émotions et de la récompense, telles que l'amygdale, l'hippocampe, l'insula, le noyau caudé et le cortex cingulaire. En revanche, la perception d'une personne non familière active principalement des régions cérébrales liées au traitement visuel et moteur, comme le gyrus ectosylvien médian, situé dans le lobe temporal (Karl et al., 2020). De plus, Thompkins et al. (2021) ont constaté une corrélation positive entre la force d'activation dans ces régions et le temps passé par les chiens à manifester des comportements dirigés vers leur humain référent (aboyer, le regarder, s'asseoir près de lui ou lui sauter dessus) lorsque les chiens étaient confrontés à une tâche insoluble, cette corrélation étant absente pour une personne non familière. Egalement, Karl et al. (2021)

ont observé une plus grande activation dans l'hypothalamus lorsque les chiens étaient témoins d'une interaction sociale positive entre le propriétaire et un autre chien par rapport à une interaction entre un humain non familier et le congénère.

En résumé, l'ensemble de ces données convergent vers l'idée que la simple présence des propriétaires peut avoir un impact sur le comportement des chiens, par influence sociale. La synchronisation comportementale des chiens sur leurs propriétaires n'implique donc pas forcément la résonance motrice, mais peut aussi engager d'autres processus cognitifs comme le référencement social. Différents circuits cérébraux peuvent donc être activés, façonnant ainsi de façon durable la réponse comportementale des chiens.

6.2.2.2. L'apprentissage par conditionnement opérant

Selon le modèle en deux étapes proposé précédemment, les connexions entre les représentations sensorielles et motrices d'un comportement sont formées par les expériences répétées d'observation et d'exécution simultanées du comportement. Les neurones miroirs, basés sur ce type de connexions, ne seraient ainsi qu'un cas particulier d'apprentissage associatif (Farmer et al., 2018). Toutefois, le rôle de l'apprentissage associatif dans la réponse comportementale des chiens envers les humains pourrait être plus simple que la formation de connexions sensorimotrices. Autrement dit, il est possible qu'un apprentissage associatif soit en jeu, mais sans implication du système miroir. Les capacités des chiens à copier certains comportements humains pourraient simplement être le fruit de conditionnement opérant. Cette forme d'apprentissage, largement démontrée chez de nombreuses espèces, associe un comportement à ses conséquences (Rehman et al., 2024). Cette association est facilitée par divers renforçateurs, tels que la nourriture ou des interactions positives (caresse ou récompense verbale par l'humain, par exemple, dans le cas du chien) (Chiandetti et al., 2016; Elgier et al., 2009, 2012; Udell & Wynne, 2010). Les chiens de compagnie, en vivant auprès de l'humain, sont par conséquent largement exposés à ces renforçateurs et peuvent facilement faire des associations comportement-récompense (Prichard et al., 2018).

Par ailleurs, les chiens accumulent une vaste expérience d'observation d'actions humaines quotidiennes, qu'ils soient capables ou non de reproduire ces actions (Lonardo et al., 2024). Par exemple, les chiens sont capables de marcher avec l'humain, mais ne sont pas capables de saisir un objet avec leur patte comme un humain le fait avec sa main. Par apprentissage associatif, les chiens peuvent réaliser des actions complémentaires aux actions observées, sans qu'une expérience motrice préalable soit nécessaire. Par exemple, les chiens suivent des indices de pointage (qu'ils ne peuvent eux-mêmes produire) en fonction de leur historique de renforcement (Elgier et al., 2009, 2012). En effet, ils répondent à ces indices, mais uniquement s'ils ont été au préalable associés à une récompense. De plus, les chiens peuvent généraliser les stimuli : ils apprennent plus rapidement à répondre à un nouvel indice, tel que le pointage distal croisé, s'ils étaient déjà renforcés pour un indice similaire (comme le pointage proximal), plutôt que pour un indice différent (comme la position du corps) (Elgier, 2012). L'apprentissage associatif pourrait ainsi sous-tendre certaines compétences cognitives canines, sans nécessiter un traitement de haut niveau des informations perçues (Mersmann et al., 2011).

Dans le contexte de la marche, il est possible que les chiens associent le comportement de marcher avec l'humain à une récompense (comme le temps partagé ou des interactions positives). La synchronisation entre les chiens et leurs propriétaires serait ainsi due au fait que les propriétaires sont des renforçateurs forts pour les chiens, et que marcher avec eux serait associé à des conséquences positives pour les chiens. Bien sûr, d'autres humains que les propriétaires peuvent également être des sources de renforcement pour les chiens. Par exemple, une personne marchant aux côtés du propriétaire peut devenir un stimulus saillant pour les chiens, ce qui expliquerait pourquoi ces derniers se synchronisent mieux avec une personne inconnue ayant interagi avec leur propriétaire (Chapitre 2). De même, dans l'expérience du Chapitre 3, on peut supposer que lorsque le propriétaire est présent dans le groupe, il est la principale source de renforcement pour le chien, mais lorsqu'il s'éloigne, les membres restants peuvent temporairement être une plus grande source de renforcement.

En résumé, l'apprentissage associatif joue un rôle central dans les compétences cognitives des chiens vis-à-vis des humains, Dans le cas de la synchronisation comportementale, cet apprentissage conduit soit à la création de neurones miroirs (par la connexion entre représentations sensorielles et motrices d'un même comportement), soit à une association entre le comportement et ses conséquences positives, telles que le temps partagé avec l'humain.

6.2.2.3. La prédiction de l'action

La prédiction de l'action, c'est-à-dire la capacité à anticiper une action observée, peut favoriser l'ajustement comportemental (Monroy et al., 2021). Lorsque les chiens interagissent avec l'humain, prédire les actions humaines peut en effet leur permettre de réagir par des actions similaires ou complémentaires, et par conséquent se synchroniser avec les humains lorsque des actions similaires sont favorisées (Kubinyi et al., 2003, 2009). Dans le cadre de la marche, les chiens peuvent anticiper la direction de déplacement des humains, facilitant ainsi leur ajustement locomoteur lors des balades.

Quelques études ont démontré cette capacité de prédiction chez les chiens. Par exemple, si les propriétaires faisaient pendant plusieurs mois le même détour pendant les balades quotidiennes, sans que cela soit associé à une récompense pour les chiens, puisqu'au contraire cela les éloignait de l'entrée du domicile, les chiens suivaient d'abord leur propriétaire ou se dirigeaient directement vers la porte d'entrée, puis finissaient par anticiper le détour en se dirigeant spontanément vers le chemin de détour (Kubinyi et al., 2003). Deux études plus récentes ont mis en évidence la capacité des chiens à anticiper la cible ou l'endroit d'une action humaine dirigée vers un but (Lonardo et al., 2023, 2024). Dans l'étude de Lonardo et al. (2023), des chiens ont regardé des vidéos d'humains se dirigeant vers un ballon et les analyses d'oculométrie ont montré que le regard des chiens se dirigeait vers l'objet avant que l'humain ne le touche, ce regard anticipatif traduisant une prédiction du but de l'action humaine. Dans leur étude en eye-tracking de 2024, lorsque les chiens observaient un humain manipuler un objet, et que cet objet était ensuite à une nouvelle position, ou qu'un nouvel objet était placé à la place de l'ancien, alors les chiens ne regardaient pas en avance le nouvel objet ou le nouvel emplacement de l'ancien

objet. En revanche, les auteurs ont observé une dilatation de la pupille des chiens lorsqu'ils regardaient le nouvel objet placé au même endroit que l'ancien objet. Les auteurs suggèrent que cette dilatation pupillaire est un indice de prédiction du lieu où sera effectuée l'action humaine.

D'après ces auteurs, cette capacité de prédiction du but ou du lieu de l'action n'est pas forcément liée à l'activation des représentations motrices de l'action en question chez le chien. En effet, les chiens présentent des comportements d'anticipation même lorsque l'action humaine ne fait pas partie du répertoire moteur des chiens (attraper l'objet à pleine main par exemple). Cela suggère que l'expérience motrice personnelle d'une action n'est pas nécessaire pour que les chiens anticipent la cible de cette action (Lonardo et al., 2024). Par ailleurs, si l'humain effectuait des mouvements proches de ceux qui sont possibles pour les chiens, se déplacer à quatre pattes vers le ballon notamment, alors les chiens présentaient moins de regard anticipateur, et passaient plus de temps à regarder l'agent humain (Lonardo et al., 2023). Les auteurs ont conclu que les mouvements non familiers – les chiens étant généralement peu habitués à observer des humains se déplacer de cette façon – ont retardé leur tendance à prédire la cible de l'action humaine. Ainsi, il semble que ce soit la familiarité visuelle avec l'action observée, plutôt que l'activation des représentations internes de l'action, qui influence la prédiction de l'action chez le chien.

Dans l'étude de la thèse portant sur l'interférence motrice (Chapitre 5), nous avons interprété l'effet de la partie du corps, obtenu lors du test d'interférence motrice mené avec l'entraînement sensorimoteur, en nous basant sur les résultats de ces études. Les chiens ont certes une expérience visuelle des gestes humains impliquant le coude, d'autant plus depuis la crise sanitaire liée à la COVID-19, mais ils ont davantage d'expériences visuelles des actions humaines impliquant les mains. En revanche, ils n'ont pas d'expérience motrice leur permettant de poser leur coude sur une cible. Par conséquent, nous avons considéré que leurs temps de réaction rallongés pour les actions humaines du coude par rapport aux actions de la main étaient le résultat d'une prédiction incorrecte de l'action humaine. Les chiens auraient ainsi anticipé une action de la main, plus probable vu leurs expériences visuelles et l'erreur de prédiction aurait perturbé l'exécution de l'action par les chiens. Ces observations sont cohérentes avec celles faites chez les nourrissons, qui, possédant des expériences visuelles mais n'ayant pas encore développé d'expériences motrices, sont quand même capables d'anticiper les actions de leur parents (Monroy et al., 2021).

Enfin, puisque des expériences visuelles semblent nécessaires pour être capable d'anticiper une action, il apparait que l'expérience joue un rôle dans la prédiction de l'action, comme pour la résonance motrice. L'apprentissage basé sur l'observation d'actions quotidiennes, telles que la saisie d'objets avec les mains, pourrait ainsi faciliter la prédiction d'actions chez le chien, même lorsque ces actions ne sont pas réalisables par le chien lui-même.

6.2.3. La synchronisation comportementale du chien sur l'humain : un cas unique reposant sur un mécanisme cognitif social universel

Certaines compétences cognitives chez les chiens sont similaires à celles présentes chez l'humain, comme la synchronisation comportementale, qui est le sujet principal de cette thèse, mais aussi l'utilisation des signaux référentiels ou la sensibilité à l'état attentionnel, pour en citer quelques-unes. Chez le chimpanzé, le plus proche parent phylogénétique de l'humain, ou le loup, le plus proche parent du chien, ces aptitudes cognitives sociales envers l'humain ne sont pas aussi développées que celles du chien, ils sont par exemple moins performants que les chiens de compagnie dans le suivi du geste de pointage pour obtenir de la nourriture (pour une revue, voir Kaminski & Nitzschner, 2013 et Lea & Osthaus, 2018).

Pourtant, le dernier ancêtre commun des chiens et des humains vivait il y a environ 95 à 100 millions d'années, les cerveaux des canidés et des primates ont donc largement évolué différemment depuis (Boch et al., 2024). Notamment, chez l'humain, les lobes frontal et pariétal, où l'on retrouve des neurones miroirs, sont beaucoup plus développés que le lobe occipital, alors que c'est l'inverse chez le chien (Garin et al., 2022). La perception des actions implique les régions pariétales et temporales chez l'humain (Hecht et al., 2013) et principalement le lobe temporal chez le chien (Boch et al., 2024). La similitude des capacités cognitives sociales entre ces deux espèces ne réside donc pas dans la similarité des structures cérébrales, puisque les réseaux d'observation de l'action ont évolué indépendamment chez les primates et les carnivores, mais repose plutôt sur une convergence fonctionnelle (Boch et al., 2023).

Dans cette discussion de thèse, nous avons proposé plusieurs mécanismes cognitifs pouvant sous-tendre la synchronisation comportementale du chien sur l'humain. Néanmoins, ces mécanismes ne sont pas spécifiques. En ce qui concerne le modèle de la résonance motrice, basée sur l'activation des neurones miroirs, des structures neuronales ayant des propriétés miroirs ont en effet été mises en évidence chez différentes espèces éloignées phylogénétiquement, dont les primates, les rongeurs et les oiseaux (voir Bonini 2022 pour une revue). Également, nous avons développé le rôle important de l'apprentissage associatif, et c'est un mécanisme largement démontré chez un très grand nombre d'espèces (Heyes, 2012). Cela suggère que la synchronisation comportementale, ubiquitaire chez les espèces sociales, reposerait sur des processus cognitifs universels, qui seraient conservés au travers de l'évolution des espèces.

En outre, une revue récente de la littérature a montré que les capacités cognitives sociales des chiens, au niveau intraspécifique, ne présentent pas un caractère unique, puisque des capacités similaires sont observables chez des espèces proches phylogénétiquement, comme le loup, ou d'autres carnivores, tels que les dauphins, ou même d'autres espèces domestiquées comme le cheval (Lea & Osthaus, 2018). Par exemple, les chiens présentent les mêmes formes simples d'apprentissage que les autres espèces de vertébrés au niveau intraspécifique, leur cognition sensorielle est également similaire à celle d'autres carnivores et chasseurs sociaux. En fin de compte, les chiens

n'ont pas démontré de capacités qui ne se retrouvent pas chez d'autres espèces sociales (Lea & Osthaus, 2018).

Si la cognition canine n'est pas si exceptionnelle, qu'est-ce qui rend alors la synchronisation comportementale entre chiens et humains remarquable et spécifique ? Sa particularité réside dans le fait qu'elle survient entre deux espèces phylogénétiquement éloignées, mais qui cohabitent dans le même environnement, avec l'une de ces espèces, l'humain, qui a exercé une pression de sélection sur l'autre, le chien. Les chiens ont hérité leur capacité de copie de comportement de leurs ancêtres sauvages, qui se synchronisaient lors d'activités de groupe, comme la chasse (Range & Marshall-Pescini, 2022). Au cours de la domestication, les humains ont sélectionné certains traits chez les chiens, pour les aider dans certaines activités comme la chasse ou la garde de troupeaux. Cette sélection a induit chez le chien la capacité à se synchroniser avec l'humain (Kaminski & Nitzschner, 2013). Ainsi, le sélectionneur (l'humain) a eu un impact sur l'évolution des compétences cognitives du sélectionné (le chien). Par ailleurs, d'un point de vue ontogénique, les chiens bénéficient d'une exposition visuomotrice précoce et prolongée à l'humain, ce qui n'est pas le cas pour d'autres espèces fréquemment étudiées en cognition comparée, comme les primates non humains ou les canidés sauvages (Heyes, 2016). Cette exposition rend possible le développement d'aptitudes cognitives particulières chez le chien, et expliquerait pourquoi d'autres espèces n'ont pas de telles compétences cognitives sociales envers l'humain (Kaminski & Nitzschner, 2013). Il reste à déterminer si ces aptitudes reposent sur des processus cognitifs de bas niveau, ou bien si des processus cognitifs plus élaborés, comme la théorie de l'esprit, sont également engagés.

En résumé, la synchronisation comportementale entre le chien et l'humain ne repose probablement pas sur des mécanismes cognitifs spécifiques aux primates ou aux carnivores, mais est rendue possible par l'enculturation et l'historique de domestication des chiens. Cela fait du binôme chien de compagnie – humain un modèle particulièrement pertinent pour étudier l'évolution de la cognition sociale et les bases cognitives de la synchronisation comportementale.

6.3. Apports pratiques pour la gestion des interactions humain-chien au quotidien

En intégrant les découvertes de la thèse avec les connaissances établies dans la littérature existante, nous pouvons identifier quatre axes d'applications pratiques de la synchronisation comportementale pour optimiser les interactions quotidiennes entre les chiens et les humains.

6.3.1. La synchronisation interspécifique pour faciliter les interactions entre les chiens et des personnes non familières

Les interactions entre les chiens et les personnes non familières peuvent s'avérer problématiques si les chiens présentent des comportements agressifs, le plus souvent résultant de la peur (Flint et al., 2017). En effet, 36,2 % des morsures de chiens sont dirigées vers des personnes non familières (Shuler et al., 2008). L'agression est le deuxième problème comportemental le plus fréquemment signalé par les propriétaires, selon l'étude de (Dinwoodie et al., 2019). Cette même étude rapporte une prévalence des comportements d'agression envers les personnes inconnues atteignant 10% au sein du domicile et 7,9 % à l'extérieur du foyer. De plus, les propriétaires sont moins enclins à s'engager dans des activités avec leur chien si celui-ci est agressif envers les personnes inconnues (Bennett & Rohlf, 2007). Cela peut conduire à une vie moins enrichissante pour le chien, et pire encore, ce problème comportemental est l'une des principales causes d'abandon des chiens en refuge (Powdrill-Wells et al., 2021). Mieux gérer les interactions entre les chiens et les personnes inconnues est donc crucial, cela constitue à la fois un enjeu de santé publique et de bien-être animal.

La gestion de ces interactions repose en partie sur le comportement du propriétaire, qui est la référence sociale des chiens. En effet, lors des rencontres avec des nouvelles personnes, le comportement du propriétaire influence directement celui du chien (Duranton et al., 2016, 2017b). Ainsi, en balade par exemple, adopter une attitude positive et détendue envers des inconnus facilite les interactions entre son chien et ces personnes. Cependant, le comportement de ces dernières joue aussi un rôle sur la réponse comportementale du chien. Nous avons montré dans cette thèse que s'ajuster sur le chien ou sur son propriétaire favorise un rapprochement physique du chien envers la personne (Chapitre 2). Il est cependant important de noter que cet effet était temporaire, puisque la moitié des chiens ont ensuite rejoint leur propriétaire avant la fin du protocole de marche en ligne droite. Cela indique que la synchronisation des chiens sur la personne n'était pas très marquée, néanmoins ces résultats offrent aux propriétaires des pistes intéressantes pour gérer les interactions avec les personnes non familières. Ces résultats sont ainsi applicables lors des rencontres entre un promeneur et un propriétaire de chien, ou dans d'autres contextes où l'ajustement de comportement peut être utilisé pour faciliter les interactions entre les chiens et les personnes non familières et réduire le risque de comportements non désirés chez le chien. Voici trois exemples concrets d'application :

- En consultation chez le vétérinaire

Les chiens manifestent souvent des signes de stress lorsqu'ils sont dans des structures vétérinaires, et les propriétaires ne sont pas toujours capables d'évaluer le niveau de stress de leur animal (Mariti et al., 2015). Ce stress peut compliquer l'examen général, en altérant certaines variables physiologiques, en augmentant le risque de morsure, voire en rendant nécessaire une anesthésie générale pour poursuivre l'investigation clinique. De plus, la peur perçue par les propriétaires chez leur animal lors d'une visite vétérinaire

constitue une des principales raisons pour lesquelles ils hésitent à consulter par la suite (Herron & Shreyer, 2014). Dans le cadre d'une consultation dont le motif n'est pas une urgence, voici ce que je recommande aux vétérinaires praticiens : commencer par s'asseoir en face du propriétaire, tout en laissant le chien explorer la salle à son rythme ; et prendre le temps de noter l'historique du chien (anamnèse) et les raisons qui ont incité le propriétaire à consulter (commémoratifs). Être assis avec le propriétaire en étant à son écoute, tout en maintenant une intonation calme, peut contribuer à réduire le niveau de stress de l'animal. Ce n'est qu'après cette étape que l'examen clinique peut commencer. Je suggère également que les vétérinaires procèdent à l'examen en s'adaptant au chien, notamment en se positionnant à côté de lui plutôt que face à lui, avec les épaules orientées dans la même direction que celles du chien, et en maintenant un comportement détendu, sans geste brusque. Enfin, il est important d'expliquer au propriétaire que son comportement influence celui de son chien. L'objectif n'est évidemment pas de le culpabiliser, mais de l'accompagner, de le rassurer et de le conseiller afin d'optimiser le déroulement de la consultation (Gazzano et al., 2008). Il est donc nécessaire de s'adapter non seulement à l'animal, mais aussi à son propriétaire, pour une prise en charge efficace. Bien que cette approche puisse sembler chronophage, je pense qu'elle est fondamentale et qu'elle peut s'inscrire dans les programmes pratiques de gestion du stress en milieu vétérinaire, qui visent à limiter le stress, le risque de blessure et le recours à l'anesthésie pour des examens de routine (Herron & Shreyer, 2014). De plus, cette approche facilitera les visites futures, réduisant ainsi le risque que le propriétaire repousse une consultation, potentiellement au détriment de la santé de son animal.

- Lorsqu'une personne non familière arrive au domicile

Comme mentionné précédemment, les comportements agressifs envers des personnes non familières sont souvent rapportés par les propriétaires, et pas seulement dans les espaces publics. Une situation fréquemment évoquée d'après mon expérience personnelle est celle des aboiements lorsque quelqu'un se trouve derrière la porte d'entrée du domicile. Bien qu'un chien qui aboie à la porte soit un comportement naturel, visant à communiquer à son maitre la présence d'un individu (Pongrácz et al., 2010), cela devient problématique lorsque les aboiements continuent après que la personne entre, voire s'accompagnent de comportements agonistes (par exemple, babines relevées, poils du dos hérissés, queue tendue, tentatives de morsures). Ma recommandation est qu'au lieu de faire entrer immédiatement la personne lorsqu'elle arrive près de la porte d'entrée, le propriétaire prenne quelques minutes pour discuter avec elle devant la porte, les deux adoptant une attitude positive et détendue, tout en ignorant le chien. Cette approche laisse l'opportunité au chien de faire l'expérience d'une interaction positive entre la personne et son propriétaire, rendant moins probable la manifestation de comportements agressifs ou excessifs ensuite. A titre d'anecdote, plusieurs participants de l'expérience portant sur la synchronisation entre le propriétaire et la personne inconnue (Chapitre 2) m'ont rapporté avoir adopté l'approche que je viens de présenter lorsqu'une personne se présentait à leur domicile. Leurs chiens ne présentaient pas de comportements agressifs (c'était un critère d'inclusion dans l'étude), mais certains avaient tendance à aboyer de manière prolongée à l'arrivée d'un visiteur. Les propriétaires ont noté que cette méthode réduisait la durée des aboiements. J'ai d'ailleurs

moi-même utilisé cette approche lorsque je me rendais chez les participants de l'expérience sur l'interférence motrice (Chapitre 5), ce qui me permettait ensuite de commencer l'apprentissage avec les chiens, en obtenant leur coopération sans difficulté.

- Pour favoriser le bien-être et l'adoption des chiens de refuge

Le placement dans un refuge est une source de stress pour les chiens (Protopopova, 2016). De plus, les refuges constituent un environnement avec peu d'opportunités d'interaction sociale (Protopopova, 2016). Dans sa thèse, Charlotte Duranton propose que le personnel de refuge s'engage dans des activités synchronisées avec les chiens, qu'un soigneur s'assoit à côté du chien dans l'enclos et regarde dans la même direction que lui par exemple, ou aille en balade avec lui. Ces interactions permettent de limiter la privation sociale et de réduire les problèmes de sociabilité des chiens en refuge. Elle suggère également que les potentiels adoptants fassent des activités synchronisées avec le chien, comme aller se balader ou jouer avec lui.

Pour des chiens qui ne sont pas forcément à l'aise avec des personnes inconnues, j'étends ces suggestions en proposant que les potentiels adoptants partagent d'abord des activités avec le soigneur du chien, sans entrer en contact direct avec l'animal. Par exemple, ils pourraient accompagner le soigneur lors des séances de nourrissage, des promenades ou des exercices d'éducation. Être présent aux côtés du soigneur, sans initier le contact avec le chien, peut favoriser une approche spontanée de l'animal. Cela peut favoriser l'adoption, puisque l'approche du chien vers la personne est une des premières raisons d'adoption (Weiss et al., 2012).

6.3.2. La synchronisation interspécifique comme outil de mesure du niveau d'affiliation entre un chien et son propriétaire

Le propriétaire est un partenaire d'interaction privilégié pour le chien (Horn et al., 2013), c'est un attracteur social et le chien se synchronise davantage avec lui qu'avec d'autres personnes. Les résultats issus de cette thèse, couplés à ceux des études antérieures, montrent que la synchronisation locomotrice entre le chien et son propriétaire se manifeste dans divers contextes, qu'ils soient en intérieur (Duranton et al., 2017c), en extérieur (Duranton et al., 2018), seuls ou en groupe (Lamontagne et al., 2023, 2024c). Cela met en évidence la robustesse de cette synchronisation interspécifique et en fait un excellent indicateur du niveau d'affiliation entre un chien et son propriétaire. En effet, un faible degré de synchronisation peut révéler une qualité d'interaction à améliorer. Je recommande ainsi aux professionnels du monde canin, les éducateurs notamment, d'inclure l'évaluation du niveau de synchronisation dans leurs bilans comportementaux lorsqu'ils rencontrent une dyade propriétaire – chien pour la première fois. Cela peut être fait lors d'une promenade par exemple (Figure 5. A.), en notant la fréquence à laquelle le chien regarde son propriétaire, revient vers lui, ou encore à laquelle le propriétaire s'arrête près du chien lorsqu'il renifle quelque chose. Si cette

synchronisation est faible, il est nécessaire d'améliorer en premier lieu la qualité des interactions entre le chien et son propriétaire, même si ce n'est pas le motif pour lequel l'éducateur a été contacté. En effet, le comportement du chien est fortement influencé par la quantité et la qualité des interactions avec l'humain (Arhant et al., 2010; Bennett & Rohlf, 2007), il est donc essentiel de prioriser cette amélioration avant d'aborder d'autres problématiques comportementales.

Non seulement la synchronisation comportementale peut servir d'outil d'évaluation, mais elle peut également être utilisée pour renforcer la qualité des interactions entre le chien et son propriétaire. En effet, nos résultats montrent que la synchronisation interspécifique est contagieuse (Lamontagne et al., 2024a,b), corroborant ainsi avec ceux de Duranton (2019a), qui indiquaient que la synchronisation renforce les liens sociaux entre le chien et l'humain. Je suggère donc d'intégrer dans les programmes de rééducation comportementale des activités impliquant de se synchroniser, comme jouer avec son chien, prendre des moments de repos en même temps que lui, s'ajuster à lui lors des balades, faire du dog dancing (Figure 5. B.) ou encore de l'agility (Figure 5. C.). De plus, comme la synchronisation comportementale est facilement observable et quantifiable, les éducateurs peuvent réévaluer le niveau de synchronisation entre le chien et son propriétaire au fil des séances, offrant la possibilité de démontrer concrètement aux propriétaires les progrès réalisés au cours de la rééducation. Ce que je viens de présenter est également applicable dans les programmes d'éducation, lorsqu'un humain adopte un chien par exemple. La pratique d'activités synchronisées va faciliter la création du lien social entre l'adoptant et son animal, et contribuera à le renforcer durablement, limitant ainsi le risque d'apparition de comportements indésirables dans la suite de la vie du chien.



Figure 5. (A) La synchronisation peut être évaluée (et réévaluée) pendant une balade. (Crédits : https://pixabay.com). Faire des activités impliquant de la synchronisation, comme **(B)** le dog dancing (Crédits : https://www.philouska.fr) ou **(C)** l'agility (Crédits : https://www.meganwilliamsphotography.co.uk) renforce les liens entre le chien et son propriétaire.

6.3.3. La synchronisation interspécifique pour gérer les chiens dans les espaces publics urbains

Pour les propriétaires vivant en milieu urbain, ils n'ont pas d'autres choix que de fréquenter des lieux publics avec leurs chiens, tels que les rues ou les parcs, ne serait-ce que pour permettre à leurs animaux de se dépenser et de faire leurs besoins, ce qui les amène à être régulièrement en présence d'autres personnes. Par ailleurs, dans nos

sociétés occidentales, les chiens sont considérés comme des membres à part entière dans les familles (Urbanik & Morgan, 2013). Il est donc essentiel que les espaces urbains incluent des zones partagées, adaptées à ces familles qui ne se composent pas uniquement d'humains, et où elles peuvent cohabiter en toute sécurité avec celles qui ne possèdent pas d'animaux.

Les réglementations dans les villes sont souvent strictes concernant la présence des chiens dans les espaces publics, et les aménagements urbains sont souvent inadéquats pour les chiens, puisque leur présence n'est pas toujours prise en compte lors de leur conception (Chen et al., 2022). Cela pousse parfois les propriétaires à contourner les règles afin d'élargir les possibilités d'activité de leurs animaux, tout en respectant les contraintes sociales de sécurité et de propreté (Gaunet et al., 2014). Au cours de la thèse, nous avons démontré que les chiens se synchronisent sur leurs propriétaires qu'ils soient ou non au sein d'un groupe (Chapitre 3). De plus, même si les chiens sont entrainés par un groupe de personnes, l'effet attracteur du propriétaire reprend le dessus. Bien que nos recherches aient été réalisées avec des petits groupes de personnes familières du chien, cette synchronisation avec leur propriétaire indépendamment de la présence d'autres personnes peut tout de même inciter les politiques et les urbanistes à repenser la place des chiens en ville, et à adapter les espaces publics en conséquence. Nos résultats peuvent appuyer les démarches des propriétaires pour obtenir des zones dédiées où les chiens peuvent satisfaire leurs besoins, s'exercer et socialiser (Gaunet et al., 2014).

Comme le souligne Gaunet et al. (2014), interdire les chiens dans les parcs ou exiger qu'ils soient constamment tenus en laisse n'est pas une solution efficace pour prévenir les nuisances liées à leur présence, celles-ci pourraient en fait être réduites par des mesures adaptées, telles que l'installation de panneaux et la mise à disposition de sacs pour déjections canines. Une approche plus pertinente pour mieux intégrer les chiens dans les espaces urbains consisterait à aménager des parcs où les chiens peuvent évoluer sans laisse. Ces espaces offrent aux propriétaires un environnement où leurs chiens peuvent interagir librement avec d'autres personnes et animaux tout en restant en contact visuel et sonore avec les propriétaires (Holderness-Roddam, 2020). Loin des nuisances sonores urbaines et de la circulation, les chiens peuvent ainsi explorer et se dépenser en toute sécurité. En effet, comme les chiens s'adaptent spontanément à leur propriétaire, ces derniers peuvent facilement garder le contrôle du comportement de leurs chiens, même sans laisse, sous réserve de l'absence de troubles du comportement chez le chien. De plus, même si les chiens s'éloignent des propriétaires pendant leurs explorations, ils finissent par revenir spontanément vers eux du fait de l'effet attracteur des propriétaires. On pourrait également envisager des parcours de santé pour chiens et humains, offrant l'opportunité aux propriétaires de faire du sport tout en partageant du temps et des activités avec leur animal, ce qui, en plus, amplifierait les bienfaits pour la santé liés à la possession d'un animal (Chen et al., 2022). En développant davantage ce type d'espaces, les villes pourraient non seulement améliorer la qualité de vie des propriétaires et de leurs chiens, mais aussi encourager une cohabitation harmonieuse avec les non-propriétaires.

6.3.4. La synchronisation intraspécifique pour favoriser l'éducation comportementale et le bien être des chiens

Les chiens vivent en étroite interaction avec l'humain, c'est d'ailleurs l'une des raisons pour lesquelles la recherche en cognition comparée s'intéresse au modèle du chien, mais il ne faut pas oublier que c'est une espèce sociale, ayant besoin de contacts intraspécifiques réguliers (Gfrerer et al., 2018; Siniscalchi et al., 2018). La présence de congénères affecte le comportement des chiens (Pedretti et al., 2024), et nous avons mis en évidence dans cette thèse la synchronisation locomotrice entre congénères familiers. Cela souligne l'importance des contacts sociaux entre chiens, qui jouent un rôle fondamental dans leur bien-être. En effet, la privation sociale chez le chien augmente le taux de cortisol, l'hormone du stress, et la fréquence de comportements agressifs (Wormald et al., 2016). A l'inverse, la présence d'un congénère réduit le stress chez le chien de compagnie (Gfrerer et al., 2018), et augmente l'activité exploratoire et diminue la fréquence des comportements répétitifs et stéréotypés chez les chiens de refuge (Corsetti et al., 2023; Lamon et al., 2021).

Une application qui en découle est l'utilisation de chiens « médiateurs » pour aider à réduire les comportements de stress et de peur chez les chiens anxieux ou récemment adoptés. Le comportement calme et détendu d'un chien médiateur peut influencer positivement le comportement d'un congénère, réduisant ainsi les manifestations comportementales de peur ou de stress par contagion comportementale. Une étude a d'ailleurs montré que l'émission de signaux d'apaisement par un chien (comme détourner le regard, se coucher sur le flanc, ou se lécher la truffe) diminue la probabilité d'apparition de signaux d'agressivité chez le congénère avec lequel il interagit (Mariti et al., 2017). Cela soutient l'idée que la synchronisation comportementale intraspécifique peut être un moyen efficace pour atténuer la peur et le stress chez les chiens.

La synchronisation intraspécifique peut également être utilisée dans la désensibilisation à des stimuli spécifiques, ou la socialisation avec les humains. Par exemple, un chien qui manifeste de la réactivité face à certains stimuli, comme des joggeurs ou des cyclistes, pourrait bénéficier de promenades en groupe avec des congénères qui ne présentent pas ces comportements réactifs. Ces chiens, indifférents au stimulus en question, pourraient alors servir de modèle pour le chien réactif. En commençant par des balades dans des environnements où la probabilité de rencontrer le stimulus est faible, puis en diversifiant progressivement les lieux pour augmenter cette probabilité, le chien réactif pourrait progressivement ajuster sa réponse comportementale à celle des chiens modèles. Ce processus d'exposition graduelle, couplé à la synchronisation comportementale avec les chiens modèles, favoriserait ainsi l'extinction des réactions indésirables.

Conclusion

Cette thèse apporte des contributions significatives sur l'étude des bases cognitives de la synchronisation comportementale entre le chien et l'humain. Les recherches menées au cours du doctorat ont mis en évidence l'effet de certains modulateurs de cette synchronisation, plus précisément ceux liés au comportement d'une personne non familière vis-à-vis du chien ou de son propriétaire, au nombre de personnes présentes et au type d'agent social. A la lumière des résultats obtenus, je propose un modèle basé sur la résonance motrice interspécifique pour expliquer l'ajustement comportemental du chien sur l'humain. D'autres potentiels processus cognitifs sont également présentés, comme l'influence sociale, surtout exercée par le propriétaire, l'apprentissage par conditionnement opérant et la prédiction d'actions.

Ces investigations ouvrent la voie à de futures recherches, tant sur le plan comportemental que neurologique. D'un point de vue comportemental, il serait intéressant d'examiner d'autres propriétés de la synchronisation comportementale, comme l'influence de la complexité de l'environnement, afin de déterminer si le lien entre ressources attentionnelles et synchronisation comportementale observé chez l'humain (Koban et al., 2019) se manifeste également chez le chien dans ses interactions avec l'humain. Sur le plan neurologique, des études en neuroimagerie, qui émergent déjà en IRM, permettront d'identifier les structures neuronales impliquées dans la perception et l'exécution d'action chez le chien. La confrontation des résultats de cette thèse avec ces futures études neurologiques aidera à identifier clairement les processus cognitifs qui sous-tendent la synchronisation comportementale interspécifique. Explorer ces mécanismes est crucial pour comprendre l'évolution de la cognition sociale et de la cognition canine en particulier. Etudier la synchronisation comportementale chez d'autres espèces domestiques, comme le chat ou le cheval, offrirait également un point de comparaison intéressant, car cela évaluerait les effets spécifiques de la domestication (ces espèces n'ayant pas été domestiquées pour les mêmes raisons). De plus, cela permettrait d'explorer la phylogénie de la synchronisation comportementale interspécifique.

Enfin, les résultats expérimentaux de cette thèse présentent de nombreuses applications pratiques, notamment dans la gestion du comportement des chiens dans les espaces publics, que ce soit en présence de personnes familières ou inconnues. Ces perspectives d'application peuvent aider les propriétaires de chiens, les professionnels du monde canin, et toute personne susceptible de rencontrer des chiens, à faciliter les interactions avec les chiens de compagnie au quotidien. Cette thèse, CIFRE, associe ainsi recherche scientifique et enjeux sociétaux liés à la présence canine.

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