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Kognitivní procesy u psů s důrazem na magnetorecepci

Disertační práce

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Prohlašuji, že jsem disertační práci na téma „Kognitivní procesy u psů s důrazem na magnetorecepci“ vypracovala samostatně s použitím uvedené literatury a na základě konzultací a doporučení školitele.

Souhlasím se zveřejněním disertační práce dle zákona č. 111/1998 Sb. o vysokých školách v platném znění, a to bez ohledu na výsledek její obhajoby.

V Praze dne ………………..2021

Podpis autora

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Obsah

1 Úvod a pojetí práce

„Zvířata mají stejné pocity jako člověk: radost a bolest, štěstí a neštěstí. Tato hnutí mysli je postihují ve stejné míře jako nás.“

Charles Darwin (1809 – 1882)

Zvířata jsou vnímající bytosti, která mohou prožívat emoce podobné lidským, avšak lidské chápání jejich emocí je do značné míry stále ještě omezené. K dokonalejšímu pochopení zvířecích emocí, k porozumění jejich vnímání reality, k poznání, jak fungují kognitivní procesy zvířat, k odhalení veškerých projevů jejich chování, přispěje každý malý střípek z mozaiky poznání o zvířecím smyslovém vnímání. Důležité je seznámit se co nejdokonaleji s jejich projevy chování a pokusit se vysvětlit i zdánlivě bezvýznamné behaviorální projevy. K objasnění všech otázek nám mohou napomáhat relativně nové vědní obory, jako jsou kognitivní etologie a smyslová ekologie zvířat. Pro přežití zvířecích druhů je podstatné, aby zvířata dokázala zpracovávat tok informací z vnějšího prostředí, aby si uměla informace zpracovat, zapamatovat a využít je při komunikaci, při hledání partnera nebo potravy, při obraně před predátory, ale aby se taktéž dokázala díky nim orientovat v prostoru a v čase. Díky smyslům a smyslovému vnímání se jim dostává dostatečné množství informací potřebných pro přežití. Kognitivní procesy, kam mimo čití a vnímání patří i učení, paměť a myšlení, umožňují zvířatům v jejich mozku na určitých úrovních intencionality podle mentální vyspělosti konkrétních druhů, nabyté informace ukládat, vyhodnocovat, zpracovávat a opětovně použít.

Ideálním „studijním vzorkem“ pro studium těchto procesů je právě pes domácí (*Canis familiaris)*. Je nejbližším společníkem člověka, tedy jako zvířecí model široce dostupný a snadno se učí novým úlohám. Ač se psy žijeme ve společných domácnostech, stále o jejich komunikačních a smyslových schopnostech nevíme vše.

V roce 2013 vyšla první studie zabývající se magnetickým alignmentem u psa domácího, která potvrdila, že psi dovedou rozeznat malé změny geomagnetického pole. Nač by jim, coby nemigrujícímu druhu, podobné informace sloužily? Vyvstává tím řada otázek, které je třeba zodpovědět. Otevřely se tak nezměrné možnosti pro další detailnější studium magnetosenzitivity u psů. K možnému, avšak ne nemyslitelnému propojení, by mohlo docházet u magnetorecepce a laterality. Ač do nedávné doby byla lateralita považována za ryze humánní projev, bylo empiricky dokázáno, že živočichové mají lateralizovány končetiny, smyslové orgány a smysly, a zejména mozkové hemisféry. Pokud dochází k lateralizaci u živočichů na úrovni mozku, je nasnadě zamyslet se nad případnou kooperací či konkurencí obou behaviorálních projevů a schopností, kterými lateralita a magnetorecepce jsou. Zcela jistě mají svůj důvod, proč jimi živočichové, a tedy i psi disponují. Na nás je, abychom se pokusili otázku „proč“ zodpovědět.

Intenzivním studiem psího chování můžeme získat mnoho nových zajímavých poznatků, které by bylo možné v budoucnu aplikovat i na další druhy obratlovců. Znalost člověka o projevech magnetosenzitivity a pochopení lateralizace živočichů na mozkové úrovni nám může přinést širší možnosti ke zkvalitnění životních podmínek chovaných zvířat nebo v ochraně a péčí o volně žijící druhy.

Předložená disertační práce je kompilací vědeckých článků zaměřených na studium magnetorecepce a laterality domácích psů. Odborné články, které jsou zde předloženy, jsou tematicky rozděleny do dvou částí podle cílů práce. Byly publikovány či jsou v současné době v recenzním řízení v impaktovaných vědeckých časopisech.

2 Cíle práce

2.1 Lateralita psů a magnetorecepce

Cílem první části disertační práce bylo sledovat stranovou vyhraněnost psů a ověřit, zda lateralita jedince by mohla mít jakýkoli vliv na případnou magnetorecepci psů. Úkolem bylo otestovat, zda psi vykazují stranovou preferenci. Pokud by u testovaných jedinců docházelo ke stranové vyhraněnosti, ověřit intenzitu této preference, porovnat ji s motorickými pokusy a otestovat, který typ laterality může mít vliv anebo provázanost s magnetickým alignmentem psů.

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2.2 Tvorba kognitivních map

Cílem druhé části práce bylo zkoumat u psů využití magnetorecepce při tvorbě kognitivních (mentálních) map. Úkolem bylo ověřit, zda psi vnímají magnetické pole Země a jestli jim pomáhá vytvořit si nebo uzpůsobit vlastní kognitivní mapy, respektive zda tyto procesy ovlivňuje. Dále popsat, jak pes dokáže využívat mentální mapy při pohybu ve známém terénu, ale i v cizím prostředí a jak je využívá k orientaci.

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3 Literární přehled

3.1 Kognitivní procesy

Kognitivní procesy jsou projevem potřebným pro přežití každého živočicha včetně člověka. Jsou podstatným a nedílným základem vědního oboru psychologie, zejména ve vztahu ke studiu psychologie člověka. Pojem kognitivní pochází z latinského výrazu *cognoscere,* což v překladu znamená poznávat, zkoumat či zkoušet. Jedná se o soubor procesů, které jsou součástí psychické struktury jedince, sloužících k identifikaci a zpracování poznatků z vnější i vnitřní reality. Kognitivní procesy jsou tvořeny dílčími pochody či procedurami a těmi jsou: příjem informací čili *vnímání*; zachování nabytých informací, což je *učení* a *paměť*; vybavení získaných informací, což představuje *paměť* a *imaginace*; přetvoření informací, jejich organizace i další využití, a to reprezentuje *myšlení*. V neposlední řadě se do kognitivních procesů zahrnuje taktéž *řeč*. Slouží jako dorozumívací a komunikační prostředek k přenosu informací (Juklová, 2010). Poslední jmenovaný kognitivní proces je obvykle připisován jen člověku, nicméně ostatní procesy jako jsou *vnímání, učení, paměť* a *myšlení* je přisuzováno na určitých stupních vědomí dle intencionality i zvířatům (Dennett, 1997). Všechny podněty a reakce z vnějšího světa mají potenciál pro zapamatování. Tím dochází k učení, což je faktor, který následně ovlivňuje fyziologické fungování a chování zvířat. Vytvoření a zapamatování si úspěšné strategie, tj. učení, usnadňuje zvířatům lepší zvládnutí a řešení neočekávaných situací a snižuje stres z potencionálního opětovného vyrušení (Broom & Johnson, 2019). Pro přežití je nezbytná taktéž paměť. Zvířata paměť užívají v mnoha životních situacích (nalezení potravy, návrat na místo rozmnožování, aj.) Pro tyto účely jim slouží i prostorová orientace, která je typem deklarativní paměti (Morris, 2013).

Broom (2010) uvádí, že kognitivní schopnosti a emocionální reakce zvířat mohou být mnohem složitější, než bylo doposud uvažováno. Prokázal, že psi, papoušci, prasata či hospodářská zvířata na farmách nebo zvířata chovaná jako společníci, jsou schopna složitějších kognitivních reakcí, avšak kognitivní schopnost u jednotlivce daného druhu nemusí nutně znamenat, že schopností disponují všichni příslušníci druhu.

Studium kognitivních procesů u lidí výrazně usnadňuje, prohlubuje, ale i ilustruje metoda zobrazování aktivity mozku pomocí magnetické rezonance (Royet & Plailly, 2004). Tu však nelze aplikovat na každé studium kognitivních procesů u zvířecích druhů.

Pozorování kognitivních procesů u zvířat je v mnohých případech postaveno na sledování jejich behaviorálních projevů v jejich přirozeném prostředí. To může být zajímavým přínosem a doplněním moderních studijních metod za použití přístrojů v laboratorním prostředí. Přispět by k tomuto poznání měl i interdisciplinární vědní obor zvaný kognitivní etologie (Bekoff, 1995).

3.1.1 Kognitivní etologie

Studiem obratlovců a jejich chováním v jejich přirozením prostředí se zabývá široká vědecká veřejnost již po staletí, avšak poměrně novým vědním oborem je kognitivní etologie. Ta je ekvivalentem kognitivních věd zabývajících se výhradně studiem člověka, jako je kognitivní psychologie. Lze s určitostí tvrdit, že na základě svých anekdotických pozorování získal první poznatky z oboru kognitivní etologie již Charles Darwin. Vědní obor jako takový vznikl a začal se rozvíjet až na přelomu 70. a 80. let minulého století. U jeho zrodu stál zoolog Donald Redfield Griffin (1915-2003), vydáním své knihy *The Question of Animal Awareness: Evolutionary Continuity of Mental Experience* v roce 1976 (Bekoff, 1995).

Kognitivní etologie je i v současnosti rychle rostoucím interdisciplinárním vědním oborem. Zabývá se studiem mentálních poznatků, zkušeností, veškerých myšlenkových procesů, racionality a vědomím u zvířat v přirozeném prostředí. V užším pojetí studuje tyto procesy i v laboratoři. Zkoumá chování, reakce a zpracování informací zvířaty při obraně před predátory, při výchově mláďat, při zajišťování potravy nebo při pociťování bolesti či slasti. Kognitivní etologie prokazuje, že zvířata disponují vědomím (Wilson & Keil, 1999). Donald R. Griffin si kladl otázku: „Jaké je to být konkrétním zvířetem?“. Měl zájem získat co nejvíce poznatků o vědomí zvířat. Zastával názor, že studium poznání zvířat a jejich zvířecích myslí v přirozeném prostředí, ale i v laboratoři, by mělo přispět k uznání kognitivních schopností i u zvířat žijících v přírodních podmínkách (Bekoff, 1995).

Dalším průkopníkem kognitivní etologie je americký filozof Daniel Dennett (*1942). Zastává názor čtyřstupňového hierarchického vědomí zvířat podle intencionality. Tu vymezuje z pohledu evoluce, kde se z neuvědomělého života, který závisel pouze na vnějších okolnostech, náhodách a štěstí, začal vyvíjet život uvědomělý. Na nejnižší stupeň řadí „darwinovský typ“, na druhý stupeň skinnerovský typ, založený na behaviorismu, na třetí tzv. „popperovský typ“ a do nejvyššího stupně tzv.

„gregoriovského“ začleňuje i člověka již se schopností myslet, používat nástroje a jazyk (Dennett, 1997).

3.1.2 Smysly a smyslové vnímání

Vnímání neboli percepce je jedním z kognitivních procesů. Je podněcováno vjemy z vnějšího nebo i vnitřního prostředí těla živočichů. Vjemy vyvolávají tzv. dostředivé impulzy, které si živočichové po dosažení určité intenzity schopni uvědomit pomocí kůry mozkové. Smyslové vnímání zahrnuje zrak, čich a chuť, hmat (včetně schopnosti vnímat tlak, teplo, chlad či bolest), sluch a rovněž vnímání polohy a pohybu. Smyslové vnímání umožňují tzv. receptory v podobě jednoduchých nervových zakončení anebo jako součást speciálních smyslových orgánů (Reece, 2011). Podle zachycení vjemů z vnějšího či vnitřního prostředí těla rozeznáváme exteroreceptory a interoceptory, popř. i proprioreceptory (Gaisler & Zima, 2018). Každý receptor je přizpůsoben, aby reagoval na konkrétní druh energie (tepelná, zvuková, světelná, chemická atd.) a tu následně přeměňoval na akční potenciál. Tím se za pomoci tzv. senzitivních neuronů přenáší vzruchy ze senzorických receptorů do mozku (Kučera, 2013).

3.1.2.1 Magnetorecepce

Magnetorecepce je zatím nejméně prostudovaným smyslem. Je studována u řady obratlovců. Zatím není zcela přesně určeno, jakým mechanismem je magnetické pole Země vnímáno, respektive o jaký speciální receptor by se mohlo jednat, a kde je v těle živočichů umístěn. Existuje několik hypotéz, které se snaží magnetorecepce vysvětlit. Tato schopnost jim pomáhá orientovat se v prostoru, například při migraci na dlouhé vzdálenosti (Gaisler & Zima, 2018). Magnetorecepce je jednou z hlavních částí práce, proto bude více rozvedena v kapitole 3.3 Magnetorecepce a její principy.

3.2 Lateralita

Lateralita není sama osobě kognitivním procesem, ale je se smysly velmi úzce propojena, zejména s percepcí. Díky podrobnému studiu laterality za poslední čtyři desetiletí není již chápána pouze jako výstřednost primátů a člověka, ale naopak byla odhalena jako vlastnost u mnoha skupin obratlovců (Rogers, 2003). Lateralita zahrnuje asymetrii mozkových hemisfér a behaviorální asymetrii, která je součástí každodenního chování zvířat (Vallortigara, 2000). U domestikovaných druhů má lateralita zvláštní význam při výcvik a handlingu a hraje roli při utváření jejich dobrých životních podmínek, například ustájení (Rogers, 2010).

Významnou otázkou, týkající se povahy laterality obratlovců je, v jakém rozsahu je lateralita generována mechanismy společnými pro všechny smysly a smyslové orgány. Z pohledu fyzického omezení např. ptáci, kteří se otočí za předmětem zájmu svým pravým okem, automaticky nastaví předmětu zájmu i své pravé ucho. A v opačném kontextu, bude-li konkrétní objekt předmětem zájmu pro jeden smysl zvířete, bude mít sklon stát se předmětem zájmu i pro ostatní smysly (Rogers, 2003). Velmi důležitým poznatkem je, že k lateralizaci dochází obvykle na úrovni mozku, i když lateralizace na úrovni periferních smyslových orgánů je rovněž možná (Gehring et al., 2012). Je ovšem otázkou, zda propojení receptorů nebo přímo smyslových orgánů s mozkovými hemisférami je *ipsilaterální,* neboli stejnostranné (receptory z levého smyslového orgánu předávají impulzy do levé mozkové hemisféry, z pravého smyslového orgánu do pravé mozkové hemisféry) či *kontralaterální* (receptory z levého smyslového orgánu předávají impulzy do pravé mozkové hemisféry a z pravého smyslového orgánu naopak do levé hemisféry).

3.2.1 Typy laterality

3.2.1.1 Mozková lateralita

Mozková lateralita je u obratlovců běžným jevem a je všudy přítomná (Gehring et al., 2012; Magat & Brown, 2009; Rogers, 2003). Dříve byla považována pouze za výlučně lidskou vlastnost, ale nyní je brána jako princip fungování mozku obratlovců (Duboc et al., 2015; Güntürkün et al., 2000). Zvyšuje výkonnost mozku v kognitivních úkolech, kdy živočich je přinucen zapojit současně, ale při tom odlišně obě mozkové hemisféry. Jako příklad je možné uvést pozornost před predátorem a vyhledávání potravy (Rogers, 2004). U řady druhů je prokázáno používání pravé mozkové hemisféry k provádění rychlých reakcí, řídí únik či nouzové reakce, slouží ke sledování všeho nového a je projevem intenzivních emocí, jako je i agrese. Levá mozková hemisféra zajišťuje třídění a klasifikaci podnětů, reakce, u kterých je vyžadováno zvážení více variant, řídí zavedené vzorce v nestresových situacích (Austin & Rogers, 2012; Rogers, 2010; Siniscalchi, 2008; Vallortigara, 2000). Siniscalchi (2008) uvádí, že funkční mozková asymetrie, tedy použití rozdílné mozkové hemisféry, byla studována hlavně z hlediska vizuálních reakcí. U primátů byla mozková asymetrie zkoumána i pro sluchové vnímání. Na základě poznatku z výzkumu laterality primátů vytvořil Siniscalchi (2008) experiment se psy s cílem určit, zda psi používají ke zpracování zvukových podnětů odlišné hemisféry. Závěr studie odhalil, že psi skutečně pro zpracování druhové vokalizace používají levou hemisféru a zvuky bouřky, která v nich může vyvolat emoce strachu, zpracovávají pomocí pravé mozkové hemisféry. Stejných výsledků dosáhl Siniscalchi et al. (2018) u psů, u nichž bylo sledováno zpracování lidských hlasů. Psi reagovali na negativní emoční vokalizaci člověka (na strach, na smutek) pravou mozkovou hemisférou, zatímco levá mozková hemisféra zpracovávala pozitivní vokalizaci (na zvukové projevy štěstí člověka).

Wylie et al. (2017) potvrzují vliv mozkové lateralizace na výsledné chování psů. Asymetrie chování, které odráží rozdílné zapojení obou hemisfér, prokazuje zapojení odlišných hemisfér mozku psa na různých funkčních úrovních, včetně senzorické a motorické. McGreevy & Rogers (2005) potvrdili, že k lateralizaci mozku koní dochází minimálně na dvou úrovních jednak na úrovni smyslové a na úrovni motorické.

3.2.1.2 Smyslová lateralita

Smyslová (senzorická, percepční) lateralita je studována na úrovni různých smyslů. Tento typ laterality může kupříkladu vyjadřovat používání pravého či levého visuálního pole živočichů při různých aktivitách. Percepční asymetrie, zejména u zvířat s laterálním umístěním očí nebo i uší, má podstatný biologický význam a je v jejich chování všudypřítomná. Tuto skutečnost dokazuje právě rozdílené používání zorného pole levého či pravého oka při různých úkolech jako je hledání potravy, ochrana před predátory či agonistické chování (Vallortigara & Rogers, 2005). Naproti tomu ve zvířecí říši existuje řada druhů s frontálním postavením očí, tedy s predispozicí pro binokulární vidění. Tito živočichové jsou pak schopni lépe vnímat ve třírozměrné vidění, avšak mají zhoršené periferní vidění. Robins & Rogers (2004) potvrdili, že i ropuchy s binokulárním viděním disponují výraznou lateralitou. Visuální lateralita byla potvrzena u řady obratlovců např. u domácích kuřat (Rogers & Anson, 1979), u holubů (Güntürkün et al., 2000), v populaci divokých australských koní (Austin & Rogers, 2012). Výrazná vizuální lateralita byla prokázána u psů. Promítáním zrakových podnětů během krmení u nich byla zjištěna vizuální asymetrie (Siniscalchi et al., 2010).

Lateralizace vnímání zvukových podnětů byla studována u zpěvných ptáků. Již na začátku sedmdesátých let pozoroval Nottebohm (1971) u pěnkav, že při svém zpěvu zapojují levou mozkovou hemisféru, zatímco ve stejné oblasti pravé mozkové hemisféry tato funkce chyběla. Siniscalchi et al. (2012) odhalili lateralizaci ve vokalizaci psů. Zjistili, že při poslechu známých zvuků natáčejí pravé ucho a tím zapojují levou mozkovou hemisféru, kdežto u nových neznámých podnětů natáčejí ke zvuku levé ucho a zapojují pravou mozkovou hemisféru.

Siniscalchi et al. (2011) se zaměřili na podrobnější výzkum senzorické laterality psů, a to na jejich dominantní smysl, kterým je čich. Čich je z hlediska laterality málo prostudovaným smyslem. Autoři sledovali použití levé a pravé nozdry na různé emoční podněty za přirozených podmínek. U nových čichových vjemů, kterými byly potrava, citron, vaginální sekret fen používali psi nejprve pravou nozdru a s postupným opakováním těchto čichových podnětů přešli na použití levé nozdry. Výsledky pokusu potvrzují asymetrii mozkových hemisfér psů, neboť nové podněty psi zpracovávali zprvu pravou mozkovou hemisférou a opakováním je začali zpracovávat jako rutinu levou mozkovou hemisférou. Když však psi čichali dráždivé podněty, jakými jsou adrenalin nebo pach potu jim známého veterináře, konzistentně zapojovali pouze pravou nosní dírku i při opakovaných podnětech. Podařilo se tak potvrdit asymetrii používání nozder (Siniscalchi et al., 2011).

Zajímavé je porovnání senzorické a motorické laterality. Tomkins et al. (2010b) navrhnuli pokus tzv. Sensory Jump Test, kdy psům zprostředkovali tři typy vidění (binokulární, monokulární vidění na pravé a monokulární vidění na levé oko) při skokovém úkolu. Autoři potvrdili, že neexistuje souvislost mezi preferencí očí a nohou. Tato skutečnost naznačuje, že preference očí není výsledkem lateralizované motorické kontroly a že preference očí a končetin je založena na dvou odlišných mechanismech a různých úrovních neurálního uspořádání (Tomkins et al., 2010b). Rozdílné úrovně nervového uspořádání smyslové i motorické laterality potvrdili i McGreevy & Rogers (2005) u koní.

3.2.1.3 Motorická lateralita

Motorická lateralita se posuzuje na základě preference použití párových končetin obratlovců v motorických dovednostech či běžných úkolech jako je třeba i chůze nebo stání. K jejímu hodnocení jsou jako nejběžnější prostředek používána pozorování zaměřená na použití hrudních končetin (Batt et al., 2007). K tomuto účelu slouží několik typů motorických testů, které sledují rozdílné zapojování obou předních končetin (Batt et al., 2007; Poyser et al., 2006; Quaranta et al., 2004; Siniscalchi et al., 2016; Tomkins et al., 2010a, 2012) Pozoruhodné jsou motorické experimenty na koních, ze kterých je možné čerpat poznatky k motorické lateralitě psů. Studie McGreevy & Rogers (2005) sledovala domácí koně a jejich preferenci umístění předních končetin jedné před druhou během pastvy. Zjistili, že u domácích koní se preference končetin, objevuje a navíc se s postupným zvyšováním věku upevňuje, což naznačuje vliv tréninku nebo neuromotorické zrání. Austin & Rogers (2012) sledovali divoké koně v Austrálii. Uvádějí, že nebyla pozorována vyhraněnost preferenčního používání končetin napříč populací. Potvrzují tak teorii, že v populaci domácích koní, kde k upřednostňování končetin dochází, může být projevem získaného chování na základě učení a zkušenosti. Austin & Rogers (2012) také objevili silnější individuální preferenci končetin u mladších divokých koní. Domnívají se proto, že získáváním zkušeností v přirozením prostředí se může vyhraněnost končetin modifikovat (Austin & Rogers, 2012).

Wells (2003) zjišťovali v práci o motorické lateralitě psů preferenci použití předních končetin a intenzitu preference ve třech různých úkolech. Odhalili, že psi a feny se odlišovali ve směrové preferenci použití tlapek. Pravé přední tlapky častěji používali feny, oproti tomu psi upřednostňovali levou tlapku, což bylo potvrzeno i v následujících výzkumech (Quaranta et al., 2004; McGreevy et al., 2010). V těchto dvou jmenovaných studiích, ale ovšem byli zapojeni do experimentu i kastrovaní psi. Potvrzuje to i několik protikladných studií, které nevykazují souvislost mezi pohlavím psů a lateralitou (Branson & Rogers, 2006; Poyser et al., 2006). Lateralizované chování u psů na úrovni motorické laterality může být silně ovlivněno druhem úkolu, který má pes konkrétně plnit. Jednotlivé motorické testy však společně nekorelovaly (Tomkins et al., 2010a).

Možnou spojitostí mezi motorickou lateralitou a imunitním systémem psů se zabývali Quaranta et al. (2004). Zkoumali vztah mezi imunitními funkcemi a preferencí tlapek psů. Motorickým testem ověřili lateralitu psů. Poté otestovali u leváků, praváků i ambilaterálních jedinců počet bílých krvinek, hladinu lymfocytů, granulocytů a monocytů. Jednalo se o vůbec první studii, která představila důkazy, že mozková asymetrie může měnit imunitní odpovědi psů při regulaci protilátky.

3.2.1.4 Strukturální lateralita

Strukturální (morfologická) lateralita se týká nesouměrností morfologie těla, jeho částí nebo tělních orgánů. Typickým příkladem je asymetrické umístění vnitřního orgánu -

srdce. Pozorovány jsou ale i strukturální rozdíly mozku, respektive jeho částí. Např. Goto et al. (2010) objevili strukturální i funkční rozdíly v hipokampu myší a jejich korelaci se schopností prostorového učení.

Strukturální lateralita je pozorována v souvislosti s anatomickými atributy vlasových vírů u lidí nebo srsťových vírů u zvířat, ty mohou být zajímavým znakem lateralizace jedince. Klar (2003) zkoumal u lidí vztah preference ruky a směru vlasových vírů. Domnívá se, že vývoj vlasových vírů u lidí vzniká již na úrovni embryonálního vývoje a má souvislost s vývojem nervového systému a mozku. Podle Jansen et al. (2007) by mohl směr víru poskytnout snadný anatomický korelát pro funkční lateralizaci mozku.

U zvířat byl tento typ laterality pozorován u koní ve vztahu k motorické lateralitě (Murphy & Arkins, 2008). Tomkins (2010) sledovala množství, umístění a směr srsťových vírů u psa. Tomkins et al. (2012) se zaměřili na porovnání všech tří typů lateralizace (motorické, smyslové a strukturální) současně. Výskyt srsťových vírů naznačil souvislost s motorickými a smyslovými schopnostmi psů. To by mohlo v budoucnu napomoci efektivněji určovat vhodné kandidáty pro výcvik třeba vodících psů. Strukturální lateralita a směr srsťových vírů by mohl být vhodným nástrojem k určování laterality psa.

3.2.1.5 Individuální a populační lateralita

Individuální lateralita sleduje lateralizaci na všech funkčních úrovních (mozkové, smyslové či motorické) u konkrétních jedinců. Intenzita lateralizace se může idividuálně lišit. To má vliv i na kognitivní procesy jednotlivce a taktéž to může ovlivnit individuální chování. Nicméně, i přes různé úrovně variací individuální laterality na úrovni druhu, populace nebo skupiny, se většina jedinců lateralizuje stejným směrem (Rogers & Kaplan, 2019).

3.3 Magnetorecepce a její principy

Magnetorecepce, neboli vnímání magnetického pole, je smysl, který nám lidem, resp. většině lidí, byl odepřen, anebo jím disponujeme pouze na nevědomé úrovni. V každém případě tento smysl byl prokázán u mnoha druhů živočichů různých taxonů (Begall et al., 2014; Eder et al., 2012; Johnsen et al., 2020; Lohmann et al., 2007; W. Wiltschko & Wiltschko, 2005) Bádáním na poli magnetorecepce se vědci zabývají již více než padesát let a zejména v posledních dvou dekádách se řada odborných publikací věnovaných magnetorecepci významně rozrostla z hlediska zkoumaných zvířecích druhů, kontextů, hypotéz a metodických přístupů.

3.3.1 Hypotézy pro percepci magnetického pole

Bylo opakovaně mnohokrát prokázáno, že živočichové dovedou vnímat magnetické pole Země, tedy že jsou magnetosezitivní. Nicméně o principu či mechanismech této smyslové schopnosti u zvířat se stále vedou odborné diskuse. Magnetoreceptory se teoreticky mohou nacházet kdekoliv v těle živočichů, protože magnetické pole je schopné proniknout do kterékoli biologické tkáně (Barnothy, 1964). Nejčastěji jsou diskutovány tyto tři mechanismy: (1) vnímání magnetického pole pomocí feromagnetických částic, (2) elektromagnetické indukce a (3) kvantový mechanismus založený na radikálových párech (Kobylkov, 2020; Mouritsen, 2018).

3.3.1.1 Princip feromagnetických částic

V přírodě se běžně vyskytuje organický magnetit (Fe_3O_4) a je součástí i tkání živočichů. Magnetit byl poprvé objeven u mořských plžů chroustnatek v jejich radule (Lowenstam, 1962). Hypotéza o feromagnetických částicích je založena na předpokladu, že v tkáních živočichů existují magnetické částice, které se chovají jako miniaturní magnetické jehly kompasu (Yorke, 1979). Geomagnetické pole na magnetické krystaly vyvíjí točivý moment, díky kterému se přiklání ke směru indukčních čar a tak se mění magnetický vstup na mechanickou energii (Kirschvink & Gould, 1981). Přítomnost magnetitových částic v tkáni živočichů dokazuje například Eder et al., (2012) u pstruhů. Magnetitové částice musí mít ale propojení s nervovým systémem, aby tento princip byl funkční. Některé studie naznačují, že magnetit je pouze vedlejším produktem metabolismu železa (Mouritsen, 2018; Winklhofer, 2007). Může se tedy jednat pouze o náznak možné magnetoreceptivní funkce (Kobylkov, 2020).

3.3.1.2 Princip elektromagnetické indukce

Elektromagnetická indukce je založena na vzájemném silovém působení magnetického a elektrického pole, měnící se magnetické pole generuje napětí na elektrickém vodiči (Kobylkov, 2020). Tento princip je předpokládán u paryb (žraloků, rejnoků) a smyslovým orgánem jsou pravděpodobně Lorenziniho ampule. Pohybuje-li se takový živočich (vodič) mořskou vodou (vodivé médium) vytváří se tak elektrický obvod s polaritou a intenzitou proudu v závislosti na rychlosti a směru pohybu ve vztahu k magnetickým siločárám. Žralok nebo rejnok tak může detekovat malé napětí, které vzniká jeho vlastním pohybem (Lohmann, 2010). Anderson et al. (2017) připevnili magnety na žraloky písečné, které jim narušily magnetický smysl, přestože indukční mechanismus by neměl být oslaben. Tento experiment s narušením proto zpochybňuje hypotézu o elektromagnetické indukci jako základním mechanismu magnetorecepce žraloků.

Pro vznik elektromagnetické indukce je potřeba pohybovat se ve vodivém prostředí. Je tedy pravděpodobné, že by primárně suchozemští obratlovci tento princip pro vnímání geomagnetického pole využívali (Ritz et al., 2010).

3.3.1.3 Princip radikálových párů

Mechanismus radikálových párů (RPM) je založen na fotochemické reakci, kde jsou radikálové páry tvořeny jako meziprodukt této reakce a jsou ovlivňovány vnějším magnetickým polem (Schulten et al., 1978). Pravděpodobně primárním magnetoreceptorem je molekula kryptochromu. Ta je schopná tvořit magneticky senzitivní radikálové páry (Ritz et al., 2010). Molekuly vnímavé na světlo mění svůj oxidační stav v důsledku absorbce světelné energie, vzniká tím chemická reakce, při které si dvě molekuly vzájemně předávají elektron a vytváří tím radikálový pár. Pakliže existují v epifýze nebo v sítnici receptory, jejichž fotopigmenty vytvářejí magneticky senzitivní radikálové páry, může magnetické pole Země přeměnit efektivitu transformace světla na membránový potenciál. Magnetické pole by se tím stalo viditelné (Ritz et al., 2010; viz též Němec & Vácha, 2007).

3.3.2 Magnetický alignment a jeho biologický význam

Jedním z projevů magnetorecepce je magnetický alignment, což je spontánní směrové zarovnání osy těla s magnetickými siločarami. Nejedná se o náhodné chování (Wiltschko & Wiltschko, 1995). Objevuje se však pouze, pokud na orientaci zvířete nepůsobí žádné jiné vnější nebo závažnější faktory, např. sklon terénu, směr příjmu informací, povětrnostní podmínky či sluneční svit. Magnetický alignment pravděpodobně poskytuje zvířatům určitou výhodu, například v danou chvíli mohou šetřit energii (Begall et al., 2013). U magnetického alignmentu zvířata nutně nemusí používat vědomou magnetickou percepci jako je třeba u navigace na velké vzdálenosti a při prostorové orientaci, magnetický alignment sám o sobě pravděpodobně funguje na podvědomé úrovni (Begall et al., 2008). Magnetický alignment byl popsánu napříč různými druhů obratlovců a v různých kontextech chování, která jsou každodenní součástí jejich života, např.: u pasoucího se skotu (Begall et al., 2008; Burda et al., 2009; Slaby et al., 2013), lovících lišek (Červený et al., 2011), v kádích u vánočních kaprů (Hart et al., 2012), vodních ptáků přistávajících na vodě (Hart, Malkemper, et al., 2013), u značkujících psů (Hart, Nováková, et al., 2013), u mladých želv (Landler et al., 2015), v útěkovém chování srnčí zvěře (Obleser et al., 2016), u divokých prasat (Červený et al., 2017), odpočívajících plameňáků (Nováková et al., 2017) nebo kontextu orientačního chování (Benediktová et al., 2020). Existují hypotézy, že zarovnání podle magnetických siločar ovlivňuje fyziologické procesy (Wiltschko & Wiltschko, 1995), pravděpodobnější je ale jeho úloha v kognitivních procesech: magnetický alignment pomáhá zvířatům synchronizovat a koordinovat pohyb ve skupině, organizovat kognitivní (mentální) mapy, měřit vzdálenost a sklon pohybu, případně i zvýšit (zaostřit) selektivní smyslovou pozornost (Burda et al., 2020). Všudypřítomné magnetické pole může přinášet vnější směrový referenční rámec (Phillips, Muheim, et al., 2010). Pozorování pastvy srnčí zvěře a hodnocení čerstvých jeleních zálehů, kde je snadno rozpoznatelná hlava a zadní část lože, naznačují, že zaznamenaný jev představuje nejen jednoduché bimodální magnetické vyrovnání osy těla, ale dokonce i orientaci hlavy na severní směr (Begall et al., 2008).

3.3.3 Magnetorecepce u psovitých šelem

Za posledních několik let bylo publikováno několik málo studií poskytujících důkazy o schopnosti psovitých šelem, lišek a psů, vnímat magnetické pole Země a případně i využívat ve svůj prospěch.

Magnetický alignment byl u psovitých šelem prvně pozorován u lišky obecné (*Vulpes vulpes)* při lovu tzv. myškováním. Podporuje teorii, že magnetické zarovnání zvířat není náhodné, ale poskytuje biologickou výhodu. Ukázalo se, že lišky byly při myškování až o 60 – 70 % úspěšnější, pokud se zarovnaly na severovýchod či jihozápad, než v jiných magnetických směrech (Červený et al., 2011). Bylo zjištěno, že psi zarovnávají osu těla podle severojižní magnetické osy Země, pokud je magnetické pole Země stabilní a nedochází jeho k rušení v důsledku geomagnetických bouří. Jednalo se o první důkaz schopnosti psů vnímat změny magnetického pole a taktéž, že magnetický alignment je jejich přirozeným behaviorálním projevem (Hart, Nováková, et al., 2013). Pes (stejně jako my) má „mentální mapu“ (srovnej např. Vesmír 96, 274, 2017/5) svého domovského okrsku či si takovou mapu v neznámém prostředí vytváří. Předpokládáme, že značkující pes zároveň zaznamenává do paměti polohu („koordináty“) označeného místa, aby toto místo a svou značku příští den zkontroloval a obnovil. Záznam polohy do mapy je snazší, když mapu orientujeme určitým směrem. Když mapu čteme a vyznačujeme do ní svou polohu, otáčíme ji také tak, že sever směřuje nahoru a sever na mapě srovnáváme s kompasem a orientačními body. Nezávislý pozorovatel přitom také uvidí, že se otáčíme. Fyzická rotace je zjevně pro nás, i pro psa, či jiná zvířata jednodušší než rotace mentální (Burda et al., 2020). V nedávné studii testující spontánní směrový výběr mezi dvěma možnostmi, psi vykazovali preferenci pro severní směr (Adámková et al., 2017). Další podporu pro magnetický smysl psů přináší i studie, kde byli psi schopni nalézt ukrytý magnetu, což nasvědčuje, že psi vykazují samovolnou nebo naučenou reakci na magnetické pole, respektive jeho narušení (Martini et al., 2018). Nejnovější studie magnetosenzitivního chování psů se zabývala prostorovou orientací loveckých psů při orientaci v terénu, kdy při návratu ke svému majiteli psi pravděpodobně dovedou využívat magnetické pole Země (Benediktová et al., 2020). Toto zjištění je další podporou významu magnetorecepce při kognitivním mapování nejen při migraci na velké vzdálenosti, ale taktéž pro prostorovou orientaci v mnohem menším měřítku (Begall et al., 2014; Burda et al., 2020; Hart, Nováková, et al., 2013).“

3.4 Kognitivní mapy

V tradičním pojetí si lze kognitivní mapu představit jako mapu prostředí, která je postupně zakládána v mozku zvířete (ale i člověka) na základě stimulů přicházejících z vnějšího prostředí. Mapa tak představuje mentální reprezentaci prostorových vztahů mezi různými objekty a mezi nimi a zvířetem (Tolman, 1948).

Pro stavbu kognitivních map je důležitá aktivní explorace prostředí (O’Keefe & Nadel, 1978). To vyžaduje dostatečně velký areál, ve kterém má zvíře možnost se opakovaně vyskytovat a cestovat za potravou, partnerem a dalšími zdroji (Peters, 1978). Přesnost mapy se zvyšuje opakováním návštěv, navigace mezi jednotlivými místy se tak stává efektivnější (Spencer, 2012). Kognitivní mapa jako neurální model vnějšího prostorového světa rovněž umožňuje generování a optimalizaci pohybu využitím zkratek a objížděk (při výskytu nenadálých překážek) (Poulter et al., 2018).

3.4.1 Prostorové informace a kognitivní mapy

Během tvorby a používání kognitivních map zvířata modifikují své chování. Např. potkani aktivně vyhledávají podněty potřebné pro konstrukci mapy. Jedná se o aktivní příjem informací (Tolman, 1948). Samotné okolní prostředí zvířete poskytuje přímé informace o jeho umístění v prostoru, vlastní pohyb zvířete může být použit pro odhad posunu pozice (Barry & Burgess, 2014). Specifické pachy prostředí se rovněž mohou podílet na tvorbě kognitivních map, nicméně jedná se o poměrně variabilní zdroj informací, který může být ovlivněn mnoha vnějšími faktory (např. vítr, sluneční záření, roční období apod.) (Peters, 1978).

S rozvojem poznatků o magnetorecepci zvířat je diskutován i další možný zdroj informací, který může poskytovat globální referenční rámec pro strukturování a organizaci kognitivních map. Magnetický alignment, jako jeden z behaviorálních projevů magnetorecepce, by mohl pomáhat zvířatům se zarovnáním mentální mapy prostředí a redukovat tak složitost lokální i dálkové navigace (Phillips, Jorge, et al., 2010). Např. u vlků (*Canis lupus*) byla potvrzena schopnost využívat při orientaci v prostoru různé zkratky a nové efektivnější trasy při návratu do výchozího místa, včetně schopnosti návratu do původního směru v případě výskytu nečekané překážky (Peters & Mech, 1976). Toto chování vlků potvrzuje používání kognitivních map v prostoru. Zajímavé je, že používání zkratek nebylo pozorováno u vlčích štěňat. Tato schopnost se objevovala postupně na základě získaných zkušeností a po opakovaných návštěvách míst v rámci jejich území (Peters, 1978). Podobné chování bylo popsáno i u loveckých psů, kteří byli rovněž schopni se vracet s využitím zkratek a nových tras, často neznámým terénem. Efektivita jejich návratových tras se výrazně zvyšovala, pokud se v první fázi návratu zarovnávali podél severojižní magnetické osy (dynamický alignment) (Benediktová et al., 2020)

3.5 Lateralita versus magnetorecepce

Levá a pravá mozková hemisféra se na anatomické úrovni vyvíjejí symetricky. Přesto v mozku existují strukturální rozdíly a každá hemisféra zpracovává konkrétní a částečně odlišné kognitivní úkoly (Duboc et al., 2015). Mozková asymetrie může ovlivňovat účinnost chování (Hirnstein et al., 2010). Myši se zvýšenou asymetrií hippokampu snížily výkony v prostorovém učení a paměti (Goto et al., 2010). Malkemper et al. (2016)

uvažují o zásadním vlivu lateralizace centrálního nervového systému na konzistentní posun magnetického alignmentu obratlovců. Shrnují podstatné hypotézy o mechanismech, které by mohly být příčinou posunu od severojižní magnetické osy. Prostorová orientace a magnetorecepce v kontextu se senzorickou lateralitou je studována posledních 20 letech. Pravděpodobně poprvé se vztahem laterality a magnetorecepce zabývali Wiltschko et al. (2002). Poskytli důkazy, že magnetický kompas ptáků je silně lateralizován a je výrazně dominantní pro pravé oko, a tedy levou mozkovou hemisféru. Hemisferické rozdíly při použití magnetického kompasu u holubů potvrdil taktéž Prior et al. (2004). Předchozí výsledky ale byly později zpochybněny (Gehring et al., 2012). S ohledem na magnetický smysl existuje pravděpodobně spíše funkční mozková lateralizace, než lateralizace na úrovni distribuce receptorů v sítnici oka (Wilzeck et al., 2010). Experiment s holuby ukázal schopnost vnímat a zpracovávat směry magnetického kompasu oběma mozkovými hemisférami. Rozdíl byl pouze ve zpracování kompasového směru. Levá mozková hemisféra upřednostňovala správný naučený směr, avšak pravá mozková hemisféra jej zaměňovala za opačný než naučený, docházelo tak k axiální odezvě. Jedná se o důkaz bilaterální funkčnosti mozku při zpracovávání magnetických informací, avšak odlišuje se kvalitou zpracování (Wilzeck et al., 2010).

Zatím existují jen velmi skrovné vědomosti o centrálním zpracování magnetických informací v mozku obratlovců. Jsou navrženy dvě hypotézy. První se opírá o mechanismus radikálových párů, kdy informace o magnetickém kompasu vstupuje z očí přes jádro thalamu do přední části mozku do tzv. Cluster N. Druhá je založená na mechanismu magnetitových částic, kde se přenáší informace o magnetické mapě z trigeminálního nervu do tzv. bazálních ganglií (ta jsou součástí koncového mozku a podílí se na řízení pohybu či na kognitivních funkcích) (Mouritsen et al., 2016). Řada obratlovců vykazuje spontánní magnetické chování, kdy se zarovnávají se severojižní magnetickou osou Země (Begall et al., 2013). Malkemper et al. (2016) dokazují významnou podobnost tohoto axiálního chování napříč rozmanitými druhy obratlovců, upozorňují ale na konsistentní posun magnetického zarovnání ve směru hodinových ručiček od geomagnetického severu. Tato odchylka magnetického alignmentu obratlovců od magnetické osy by mohla být způsobena buď lateralizací na úrovni receptoru anebo na úrovni funkční asymetrie mozku. U většiny studovaných obratlovců je předpokládáno, že disponují oběma typy magnetorecepce. Pokud by se jednalo o použití magnetického kompasu (radikálové páry), živočich by musel receptor (pravděpodobně oko) srovnat s magnetickými siločarami a následně by mohl číst ze své mentální mapy, což by mohl být důvod konzistentního posunu magnetického zarovnání u obratlovců (Phillips et al., 2002).

4 Publikované práce a práce v redakčním řízení

4.1 Lateralita psů a magnetorecepce

4.1.1 Směrová preference psů: Lateralita a „tah severu“

PLOS | ONE

RESEARCH ARTICLE

Directional preference in dogs: Laterality and "pull of the north"

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Obr. č. 1: Výřez článku Directional preference in dogs: Laterality and „pull of the north“. ***Celý článek je umístěn v příloze č. 1 této disertační práce.***

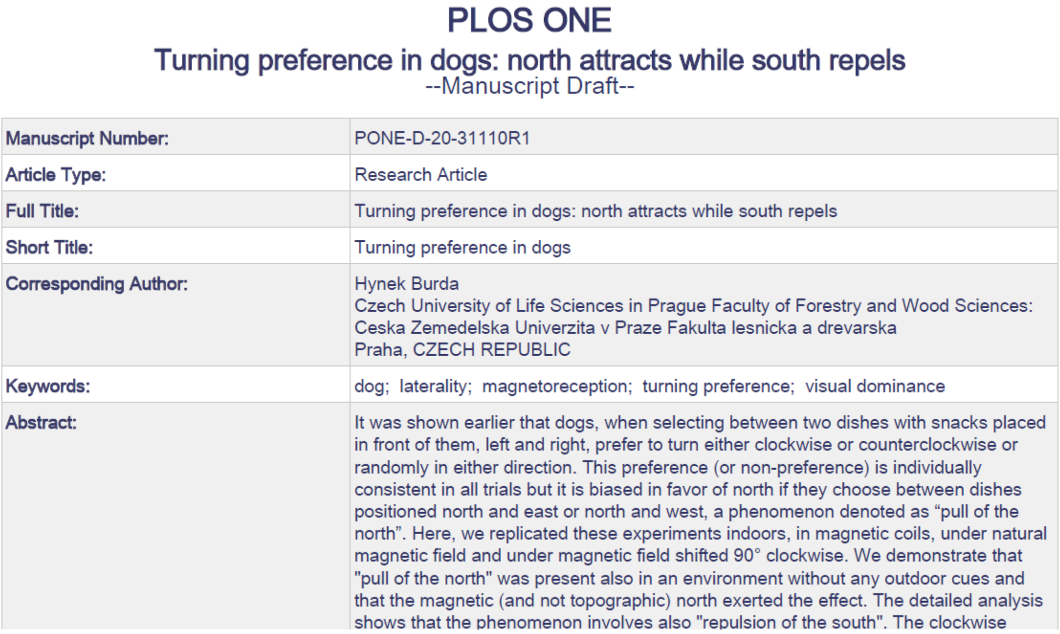
Lateralita je poměrně dobře prostudovaným jevem zejména u člověka, ale i ostatních primátů. Preference párových smyslových orgánů a párových částí těla je naprosto přirozenou věcí a v posledních letech je lateralita intenzivně sledována rovněž u psů. Vědeckými týmy z Austrálie a Itálie navrhly motorické či senzorické pokusy, kterými lze lateralitu u psů testovat. Psi se stávají předmětem zájmu i z pohledu zkoumání předpokládané schopnosti zvířat vnímat magnetické pole Země, tzv. magnetorecepce. V práci Adámková et al., (2017) je testován vliv magnetického pole Země na lateralitu psů.

Testovali jsme 25 psů, 14 různých plemen v 31 lokalitách České republice a Německu. Psi volili mezi dvěma identickými miskami se stejnou potravou, které byly umístěny nalevo a napravo od psa. Misky byly otáčeny tak, aby jejich umístění postupně vystřídalo všechny světové strany. Psi si z dvojice misek spontánně vybrali vždy jednu jako první. Někteří psi se při experimentu projevili jako pravostranní, někteří jako levostranní, část z nich se projevila jako ambilaterální, tedy nepreferující levou ani pravou stranu.

Překvapivým objevem byl tzv. „tah severu“. V situaci, kdy si psi volili výběr mezi miskami s pokrmem umístěnými na sever a východ, upřednostňovali „severní“ misku, bez ohledu na to, zda byli „praváci“ nebo „leváci“. Toto chování se výrazněji projevovalo u malých a středních plemen, fen a starších jedinců při výběru mezi miskami umístěnými na sever a na východ. Naopak vliv "tahu severu" u mladých jedinců a samců byl nesignifikantní a při výběru misek převažoval vliv individuální laterality.

ADÁMKOVÁ, J.; SVOBODA, J.; BENEDIKTOVÁ, K.; MARTINI, S.; NOVÁKOVÁ, P.; TŮMA, D.; KUČEROVÁ, M.; DIVIŠOVÁ, M.; BEGALL, S.; HART, V.; BURDA H. 2017: Directional preference in dogs: Laterality and "pull of the north". PLOS ONE, 12 (9): e0185243. DOI: 10.1371/journal.pone.0185243.

4.1.2 Preference otáčení psů: sever přitahuje, zatímco jih odpuzuje



PLOS ONE

Turning preference in dogs: north attracts while south repels

--Manuscript Draft--

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Article Type:	Research Article
Full Title:	Turning preference in dogs: north attracts while south repels
Short Title:	Turning preference in dogs
Corresponding Author:	Hynek Burda Czech University of Life Sciences in Prague Faculty of Forestry and Wood Sciences: Ceska Zemedelska Univerzita v Praze Fakulta lesnicka a drevarska Praha, CZECH REPUBLIC
Keywords:	dog; laterality; magnetoreception; turning preference; visual dominance
Abstract:	It was shown earlier that dogs, when selecting between two dishes with snacks placed in front of them, left and right, prefer to turn either clockwise or counterclockwise or randomly in either direction. This preference (or non-preference) is individually consistent in all trials but it is biased in favor of north if they choose between dishes positioned north and east or north and west, a phenomenon denoted as “pull of the north”. Here, we replicated these experiments indoors, in magnetic coils, under natural magnetic field and under magnetic field shifted 90° clockwise. We demonstrate that "pull of the north" was present also in an environment without any outdoor cues and that the magnetic (and not topographic) north exerted the effect. The detailed analysis shows that the phenomenon involves also "repulsion of the south". The clockwise

Obr. č. 2: Výstřižek článku Turning preference in dogs: north attracts while south repels – přijatý k publikování od 11. 1. 2021. ***Celý článek je umístěn v příloze č. 2 této disertační práce.***

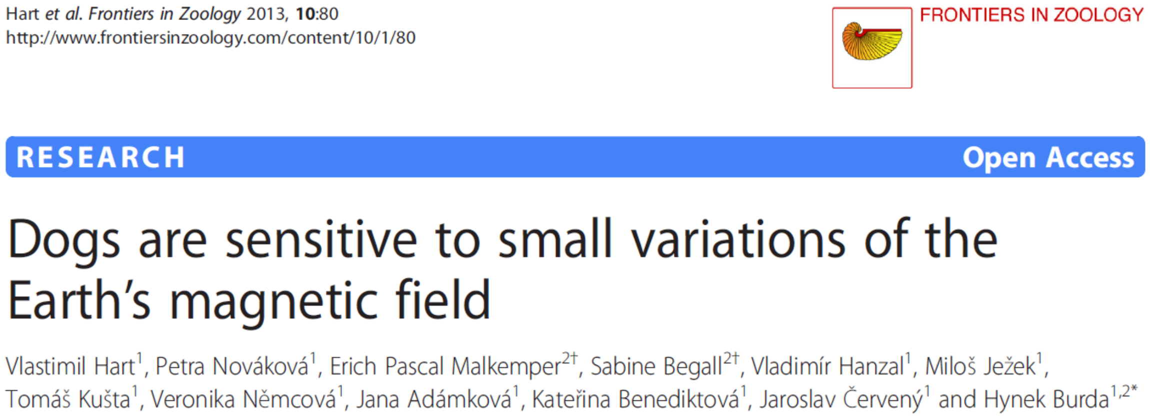
Na základě publikované studie o směrové preferenci psů ve vztahu k lateralitě a „tahu severu“, kdy se směrové preference u jednotlivých jedinců ukazují jako konzistentní, ale nasvědčují upřednostnění ve prospěch magnetického severu (Adámková et al., 2017), jsme se zaměřili na další zkoumání této problematiky. Pokud by projevy laterálního chování psů narušilo magnetické pole Země nebo uměle vytvořené magnetické pole, dalo by se hovořit o dalším dokladu existence magnetosenzitivity psů.

Experiment byl zopakován v elektromagnetické cívce za přirozeného magnetického pole a za cíleně posunutého magnetického pole o 90° ve směru hodinových ručiček. Výsledky ukázaly, že „tah severu“ ovlivňuje chování psů i v uměle posunutém magnetickém poli. Zajímavým zjištěním taktéž bylo, že upřednostnění otáčení psů ve směru hodinových ručiček (pravotočivých psů), je výraznější u kombinace umístění misek na jih a západ. Naopak u psů upřednostňujících otáčení v protisměru hodinových ručiček (levotočivých psů) je výraznější u kombinace misek umístěných na jih a východ. Z tohoto důvodu jsou misky umístěné na jih vybírány coby první méně často. Předpokládáme, že volba misky a tedy upřednostnění otočení doprava/doleva je vedena dominantním okem psa. Tato skutečnost podporuje hypotézu, že magnetorecepce u psů je založena na principu radikálových párů.

ADÁMKOVÁ, J.; BENEDIKTOVÁ, K.; SVOBODA, J.; BARTOŠ, L.; VYNIKALOVÁ, L.; NOVÁKOVÁ, P.; HART, V.; PAINTER, M. S.; BURDA, H. 2021: Turning preference in dogs: north attracts while south repels. PLOS ONE, (in print).

4.2 Tvorba kognitivních map

4.2.1 Psi jsou citliví na malé změny magnetického pole Země



Hart *et al. Frontiers in Zoology* 2013, **10**:80
http://www.frontiersinzoology.com/content/10/1/80

FRONTIERS IN ZOOLOGY

RESEARCH Open Access

Dogs are sensitive to small variations of the Earth's magnetic field

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Obr. č. 3: Výřez článku Dogs are sensitive to small variations of the Earth´s magnetic field. ***Celý článek je umístěn v příloze č. 3 této disertační práce.***

Magnetorecepce savců je již dlouho sledovaným jevem, ale až v posledních letech je pozornost intenzivněji zaměřena přímo na pozorování magnetorecepce u psovitých šelem, zejména pak u psů. Ukázalo se, že zajímavým nástrojem pro studium magnetosenzitivity je magnetický alignment, tedy zarovnání těla jedince se severojižní osou Zemského magnetického pole. Tento projev pozičního chování pravděpodobně nejen psům, ale i řadě dalších obratlovců, přináší výhodu pro jejich prostorovou orientaci a případnou tvorbu a čtení kognitivních map.

Pro splnění tohoto dílčího cíle byli sledováni psi při urinaci a defekaci, tedy u běžných činností, které denně musí psi vykonávat v rámci tzv. venčení a kdy si tímto způsobem značkují i domovský okrsek, resp. navštívená místa. Po dobu dvou let byla sbírána data celkem od 70 psů, 37 plemen. Data byla následně rozdělena podle změn intenzity magnetického pole, které byly odečítány z denních magnetogramů. Bylo prokázáno, že psi při značkování mají tendenci natáčet tělo podle severojižní osy magnetického pole Země. Toto chování se však u nich projeví jen tehdy, když je magnetické pole klidné. Z daných pozorování lze usuzovat, že psi jsou schopni vnímat velmi citlivě změny magnetického pole Země. Tento poznatek odkryl široké možnosti pro další intenzivnější bádání na poli magnetorecepce u psa domácího.

HART, V.; NOVÁKOVÁ, P.; MALKEMPER, E. P.; BEGALL, S.; HANZAL, V.; JEŽEK, M.; KUŠTA, T.; NĚMCOVÁ, V.; **ADÁMKOVÁ, J**.; BENEDIKTOVÁ, K.; ČERVENÝ, J.; BURDA, H. 2013: Dogs are sensitive to small variations of the Earth's magnetic field. Frontiers in Zoology, 10: 80. DOI: 10.1186/1742-9994-10-80

4.2.2 Magnetické zarovnání zvyšuje účinnost homingu loveckých psů

RESEARCH ARTICLE

Magnetic alignment enhances homing efficiency of hunting dogs

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Obr. č. 4: Výřez článku Magnetic alignment enhances homing efficiency of hunting dogs. ***Celý článek je umístěn v příloze č. 4 této disertační práce.***

Vytváření vlastních mentálních neboli kognitivních map, je pravděpodobně jedním z nástrojů, které napomáhají živočichům k orientaci v prostoru při hledání potravy, hledání partnera či při prostorové orientaci ve vlastním teritoriu a navigaci v neznámém prostředí.

Na základě poznatků z práce Hart et al. (2013), kde byl sledován magnetický alignment psů, vyvstala zajímavá otázka. Jsou-li psi schopni vnímat změny magnetického pole Země, nevyužívají tuto dovednost při prostorové orientaci? Lovečtí psi v myslivecké praxi se běžně vzdalují od svých majitelů na velké vzdálenosti, dokonce i ve zcela neznámém prostředí, kde se nikdy dříve nepohybovali, a přesto jsou schopni se neztratit a najít cestu zpět k majiteli. Přes tři roky bylo sledováno 27 loveckých psů při jejich návratu zpět k majiteli po jejich předchozím útěku za zvěří. Pomocí videokamer a GPS obojků bylo zjištěno, že psi při využívali dvě odlišné návratové strategie. Návrat po vlastní stopě tzv. „tracking“, anebo návrat novou trasou tzv. „scouting“. Odhaleno bylo zajímavé, dříve nepopsané chování psů, které bylo pojmenováno jako „kompasový běh“. Psi, kteří se vraceli za pomocí scoutingu, započali svůj návrat krátkým během podél severojižní magnetické osy a to bez ohledu na to, kterým směrem se nacházel jejich majitel. Je proto vysoce pravděpodobné, že psi díky provedení „kompasového běhu“

vyrovnávali svou vlastní mentální mapu prostředí s magnetickým kompasem, což by mohlo napomáhat k nastavení správného směru k majiteli.

BENEDIKTOVÁ, K.; **ADÁMKOVÁ, J**.; SVOBODA, J.; PAINTER, M., S.; BARTOŠ, L.; NOVÁKOVÁ, P.; VYNIKALOVÁ, L.; HART, V.; PHILIPS, J.; BURDA, H. 2020: Magnetic alignment enhances homing efficiency of hunting dogs. eLife, 9:e55080. DOI: 10.7554/eLife.55080

5 Diskuze

Experimenty s umisťováním misek s potravou ve dvou sousedních kompasových směrech (sever a východ, východ a jih, jih a západ nebo západ a sever) potvrdily výsledky dřívějších senzomotorických studií, že psi disponují levo/pravo-stranovou vyhraněností anebo se jeví jako ambilaterální (Siniscalchi et al., 2016, 2017; Tomkins et al., 2010a; Wylie et al., 2017).

Směrová preference otáčení psů nekoreluje s motorickou lateralitou zjišťovanou pomocí tzv. Kong testu. Zdá se, že oba typy preferencí jsou řízeny různými proximátními mechanismy. Tento závěr je v souladu s dřívějšími nálezy (Tomkins et al., 2010b), které ukazují, že vizuální (smyslová) a končetinová (motorická) lateralita psů jsou na sobě nezávislé.

Ve studiích rovněž nebyl zjištěn žádný významný vliv pohlaví na směrovou preferenci otáčení, což potvrzuje dříve publikované závěry (Branson & Rogers, 2006; Poyser et al., 2006). V souladu s výsledky studie v otevřeném terénu (Adámková et al., 2017) byla preference otáčení konzistentní pro každého konkrétního psa pro všechny kombinace umístění misek také při testování v interiéru elektromagnetické cívky. Elektromagnetická cívka má jednotné stěny, bez zjevných orientačních bodů a současně jsou zde vyloučeny vnější vlivy jako slunce nebo vítr. Oba experimenty v exteriéru (Adámková et al., 2017) i interiéru (Adámková et al., 2021) vykazovaly mírné, ale významné narušení v tom, že misky umístěné na sever byly voleny častěji, než by se dalo očekávat podle průměrné preference otáčení každého konkrétního psa. V kontextu studie je nejdůležitější zjištění, že zmíněnou preferenci otáčení ovlivnil sever magnetický nikoli topografický. Podrobná analýza však ukazuje, že „tah severu“ je složitější fenomén zahrnující také „odpuzování jihem“. Tyto efekty jsou jednostranné: preference otáčení ve směru hodinových ručiček (psi praváci) je výraznější („zrychlená“) v kombinaci jih-západ, zatímco preference otáčení proti směru hodinových ručiček (psi leváci) je „zrychlována“ v kombinaci jih-východ. Na druhou stranu kombinace sever-východ snižuje („zpomaluje“) preferenci otáčení ve směru hodinových ručiček (psi praváci), zatímco v kombinaci (sever-západ) je preference otáčení proti směru hodinových ručiček (u psů leváků) snížena. Tímto způsobem jsou celkově jižně umístěné misky s pokrmy voleny méně často, než by se dalo očekávat, zatímco severně umístěné pokrmy jsou zjevně výhodnější. Protože „rotační zpomalení“ je silnější v N-E než kombinace N-W, zatímco „zrychlení“ je silnější v S-E než v S-W kombinaci, výsledná teoretická střední preference je pro severovýchod.

V této souvislosti může být podstatné, že analýza publikovaných výsledků chování magnetického zarovnání u různých druhů obratlovců odhalila, že magnetický alignment se obvykle shoduje s magnetickou osou sever-jih, avšak průměrné směrové preference jednotlivce nebo skupin organismů jsou často posunuty ve směru hodinových ručiček od osy sever-jih (Begall et al., 2013; Burda et al., 2020; Malkemper et al., 2016). Odchylka od magnetické osy sever-jih by mohla vzniknout na různých úrovních senzorické hierarchie: mohla by souviset buď s asymetrií na úrovni smyslu, nebo s funkčními asymetriemi mozku, tj. s centrálním zpracováním.

Ačkoli způsob vnímání směru magnetického kompasu u zvířat zůstává záhadný (Nordmann et al., 2017), nálezy z behaviorálních, histologických, neuroanatomických a elektrofyziologických studií vedly k několika široce přijímaným modelům, které by mohly platit i pro magnetorecepci psů. V literatuře jsou nejčastěji diskutovány dva mechanismy: mechanismus založený na magnetitech a mechanismus radikálových párů. Snad intuitivně nejpřitažlivějším mechanismem k vysvětlení magnetosenzitivity u zvířat je myšlenka malého permanentního magnetu uvnitř těla zvířete, který funguje jako jehla kompasu (Yorke, 1979). Receptory na bázi magnetitu mohou být umístěny kdekoli v těle živočichů, nemusí být koncentrovány v párových orgánech a mohou být velmi malé.

Další navrhovaný mechanismus pro magnetorecepci u zvířat je založen na fotochemické reakci, kde jsou radikálové páry tvořeny jako meziprodukt této reakce a jsou ovlivňovány vnějším magnetickým polem (mechanismus radikálových párů) (Hore & Mouritsen, 2016; Ritz et al., 2000). Je pravděpodobné, že se vyskytují ve specializovaných buňkách sítnice (Worster et al., 2016).

Předpokládá se, že magnetické pole může generovat „vizuální“ obraz s různou intenzitou světla, barvou anebo kontrastem překrývajícím obvyklý vizuální vjem (Phillips, Jorge, et al., 2010; Solov’yov et al., 2010). Tato hypotéza naznačuje, že vizuální zobrazení severního nebo jižního směru je jasněji rozpoznatelné než zobrazení východního nebo západního směru. Lze tedy říci, že „tah severu“ by se dal interpretovat i jako „odklon / odpuzování východem nebo západem“. Protože experiment první volby misky je založen na vizuálním vnímání, můžeme postulovat, že preference otáčení byla určena dominantním okem. Dominance pravého oka měla za následek preferenci otáčení ve směru hodinových ručiček a dominance levého oka preferenci otáčení proti směru hodinových ručiček. Za předpokladu, že magnetorecepce u psovitých je založena na mechanismu radikálových párů (Červený et al., 2011; Nießner et al., 2016), lze očekávat „konflikt zájmu“, pokud se dominantní oko odvrací od severu, ale kontralaterální oko „vidí sever“. To by mohlo vyvolat potřebu nasměrování dominantního oka k severu a tím podnítit zarovnání těla podél osy sever-jih. K potvrzení hypotézy vizuální dominance by měli být psi otestováni nezávislým testem, např. sensory jump test (Tomkins et al., 2010b).

Magnetický alignment by mohl poskytovat globální referenční rámec, který by pomáhal strukturovat a organizovat prostorové chování a vnímání živočichů v mnoha prostorových úkolech. Jednou z navrhovaných možností je zarovnání kognitivní mapy podle magnetického kompasu (Hart, Nováková, et al., 2013), což by mohlo snižovat složitost místní a dálkové navigace a zmenšovat nároky na prostorovou paměť (Phillips, Muheim, et al., 2010). Jedná se o analogii použití papírové mapy člověkem. Navigace je mnohem jednodušší a intuitivnější, když se osoba zarovná s fyzickou mapou, než když by si otáčení mapy představovala a promítala mentálně. Navrhujeme, že magnetický alignment zprostředkovává fyzické zarovnání mentální mapy zvířat s ohledem na magnetické pole Země (Burda et al., 2020; Hart, Nováková, et al., 2013). Tato relativně jednoduchá strategie zarovnání by mohla pomáhat zvířatům spolehlivě a přesně „číst“ jejich kognitivní mapy.

Dalším popsaným využitím magnetického alignmentu u psů je provedení tzv. „kompasového běhu“ v počáteční fázi jejich návratu k majiteli po útěku za zvěří. Psi se při „kompasovém běhu“ zarovnávali podél severojižní magnetické osy (dynamický alignment), čímž byli schopni využívat zkratek a přímějších tras. Výrazně tak zvyšovali efektivitu návratových tras v porovnání s návraty, kdy kompasový běh neprovedli (Benediktová et al., 2020). Podobné chování, tj. schopnost využívat při orientaci v prostoru různé zkratky a nové efektivnější trasy, bylo popsáno i u blízkých příbuzných psů, u vlků (Peters & Mech, 1976). Tato schopnost se objevovala postupně na základě opakovaných návštěv různých míst v rámci jejich území a postupným získáváním zkušeností (Roger & Peters, 1978). Výše shrnuté poznatky přinášejí důkazy schopnosti psů vytvářet a používat mentální (kognitivní) mapy pro orientaci ve známém i neznámém prostředí. Jasně ukazují na zapojení magnetorecepce při používání kognitivních map, protože v případě, kdy se psi v počáteční fázi návratu nezarovnali, jejich návratová trasa byla delší a méně přímá (Benediktová et al., 2020).

6 Závěr

Předkládaná disertační práce přináší nové poznatky na poli behaviorálního chování zvířat ve vztahu k magnetorecepci:

- Chování psů při značkování domovských okrsků přineslo první důkaz o magnetosenzitivním chování domácích psů a o schopnosti vnímat malé změny magnetického pole Země.
- Prezentovaný jednoduchý test výběru ze dvou misek potvrdil magnetosenzitivitu psů a možný vliv magnetorecepce na jejich lateralitu. Mohl by být v budoucnu zařazen k dalším senzomotorickým testům pro zjištění lateralizovaného chování psů v konkrétních úkolech.
- Lateralita, „tah severu" a „odpuzování jihu" jsou jevy, které by měly být brány v úvahu při různých behaviorálních testech, s nimiž mohou být psi nebo jiná zvířata konfrontována.
- Magnetické pole Země může psům (a obecně savcům) poskytnout univerzální referenční rámec, který je nezbytný pro navigaci na dlouhé vzdálenosti a napomáhat spolehlivému „čtení" kognitivních map.

Fenomén magnetorecepce je nezbytné brát v úvahu ve studiích zaměřených zejména na prostorové chování zvířat. Naše zjištění ukazují důležitost dalšího výzkumu na zapojení magnetických stimulů u psovitých v kontextu nejrozmanitějších behaviorálních úloh.

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8 Přílohy

8.1 Příloha č. 1

PLOS | ONE

RESEARCH ARTICLE

Directional preference in dogs: Laterality and "pull of the north"

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Abstract

Laterality is a well described phenomenon in domestic dogs. It was shown that dogs, under calm Earth's magnetic field conditions, when marking their home ranges, tend to head about north- or southwards and display thus magnetic alignment. The question arises whether magnetic alignment might be affected or even compromised by laterality and vice versa. We tested the preference of dogs to choose between two dishes with snacks that were placed left and right, in different compass directions (north and east, east and south, south and west or west and north) in front of them. Some dogs were right-lateral, some left-lateral but most of them were ambilateral. There was a preference for the dish placed north compared to the one placed east of the dog ("pull of the north"). This effect was highly significant in small and medium-sized breeds but not in larger breeds, highly significant in females, in older dogs, in lateralized dogs but less significant or not significant in males, younger dogs, or ambilateral dogs. Laterality and "pull of the north" are phenomena which should be considered in diverse tasks and behavioral tests with which dogs or other animals might be confronted. The interaction and possible conflict between lateralization and "pull of the north" might be also considered as a reason for shifted magnetic alignment observed in different animal species in different contexts.

Introduction

Laterality, i.e. the predictable, non-random preference for using one side of the body (limbs, brain hemisphere, sensory organs) spontaneously or if forced or restricted to choose between two sides has been intensively studied and is well described in humans but it seems to be also a widespread phenomenon among animals. Laterality may be inborn, imprinted or entrained and has to be taken into account in maze and behavioral two-choice animal experiments [1–5]. The laterality effect is often tested (and excluded) by counting the animals' choice for either side of a T- or Y-maze under control conditions (e.g. without a stimulus or reward) and/or under conditions where the stimulus or reward is randomly alternating between both arms of the maze. While such a behavioral test for laterality (and the exclusion of its effect) is a

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standard in two-choice-experiments of this kind, potential preference for a certain (magnetic) compass direction remains usually unconsidered, and this in spite of the fact that magnetic compass preference (displayed in the so-called magnetic alignment) has been documented in a wide array of animal species in diverse behavioral contexts, reviewed in [6–10]. On the other hand, however, laterality effects should be considered also in studies dealing with compass orientation and navigation [9].

Recently, we have shown that dogs, under calm Earth's magnetic field conditions, when marking their home ranges tend to head about north- or south-wards and display thus magnetic alignment [10]. In that particular study, a test for laterality was not relevant and not necessary to exclude the existence and significance of magnetic alignment. Nevertheless, we cannot exclude that laterality played a role under some circumstances and could have influenced the angularity of the response—e.g. does a "left-handed" dog turn southwards if it comes from east but northwards if it comes from the west? Laterality in dogs was examined behaviorally in more than 20 studies e.g. [11–23]. The most commonly used motor test was the so-called "Kong test", in which the preference for a paw holding a Kong (a toy stuffed with food, KONG Company) is recorded. This laterality test is most probably not influenced by magnetoreception, cannot be masked by it but, at the same time, cannot be used to address the question whether laterality affects directional preference in the context of long-distance locomotor spatial orientation. However, there are also some other tests of lateralization—e.g. preference to approach food items placed either right or left of the dog [12] and studies of performance requiring movement in a prescribed direction [23] which can theoretically be affected or even be compromised by magnetic alignment.

Materials and methods

No permits were required for the described study, which complied with all relevant regulations. All the dog owners were informed about the study, consented with the set-up and use of their dog(s) and were present at trials.

Altogether 25 dogs (12 M, 13 F) of 14 breeds, aged on average 5.3 (SD 3.3, 1–12) years were tested in the Czech Republic (12 dogs) and in Germany (13 dogs) (Table 1, S1 Table). The 12 dogs in the Czech Republic were tested at altogether 23 localities (distinct cities and country districts, each dog in 36 test series at each locality), the dogs in Germany were tested at altogether eight localities, each dog in 20 test series at each locality. At each locality, the dogs were tested at at least two different sites. Test series were performed at different places at each site, at different days over several months, at different times of the day, so that tests with each dog evenly covered all daytimes. In all the cases, study sites were open fields, away from communications, buildings, high voltage power lines and conspicuous landmarks. Altogether 1,088 test series were performed.

Each test series involved 4 trials where the dog should make a choice between two identical dishes placed in front of it, at a distance of 2–6 m, according to the size of the dog, so that it could not look into the dishes from its starting point. The dishes were placed in an angle plus and minus 45° from the starting point, so that one dish was e.g. eastwards of the dog and the second one was placed southwards. Each test series involved four trials (test combinations): north versus east, east versus south, south versus west, and west versus north. The sequence of the tests was changed randomly. Both dishes contained identical dog snack. The dog could not see the preparation of the test, i.e. the placement of the dishes. The dog was brought to the starting point and waited to get permission to go to the dish (of its choice). Two experimenters were involved in this test. The first experimenter was setting up the test, while the dog owner (who was uninformed about the actual directions of the dishes and gave the voice command)

Table 1. Survey of the tested dogs and their factors.

breed	subject	country	size	sex	age	laterality	n test series	μ (1st locality)	μ (2nd locality)
borzoi	Hen	CZ	L	M	1	left	36 + 36	**225°**	**135°**
labrador retriever	Mon	CZ	L	M	12	ambi	36	**72°**	**x**
wirehaired pointer	Aja	CZ	L	F	4	ambi	36 + 36	**220°**	**305°**
beagle	Azi	CZ	M	M	4	right	36 + 36	**354°**	**45°**
cocker spaniel	Bar	CZ	M	F	2	left	36 + 36	**353°**	**18°**
cocker spaniel	Nel	CZ	M	F	8	ambi	36 + 36	**281°**	**278°**
foxterrier	Fre	CZ	M	F	1	left	36 + 36	**54°**	**333°**
foxterrier	Gof	CZ	M	F	1	left	36 + 36	**45°**	**62°**
foxterrier	Bes	CZ	M	F	6	right	36 + 36	**18°**	**349°**
dachshund	Ter	CZ	S	F	4	ambi	36 + 36	**270°**	**257°**
dachshund	Can	CZ	S	F	6	ambi	36 + 36	**323°**	**315°**
dachshund	Ven	CZ	S	F	9	right	36 + 36	**349°**	**333°**
border collie x münsterlander	Paa	GER	L	F	9	ambi	20	**146°**	**x**
bullterrier	Gis	GER	L	F	10	ambi	20	**135°**	**x**
flat-coated retriever	Fje	GER	L	M	2	ambi	20	**270°**	**x**
labrador retriever	Lor	GER	L	M	3	ambi	20	**180°**	**x**
labrador retriever x rottweiler	Jim	GER	L	M	3	ambi	20	**90°**	**x**
labrador retriever x rottweiler	Sam	GER	L	M	3	ambi	20	**135°**	**x**
labrador retriever	Pal	GER	L	M	5	ambi	20	**101°**	**x**
labrador retriever	Lot	GER	L	F	7	left	20	**54°**	**x**
jack russel terrier	Jac	GER	M	M	12	left	20	**31°**	**x**
chihuahua	Att	GER	S	M	3	right	20	**72°**	**x**
chihuahua	Ger	GER	S	M	4	right	20	**0°**	**x**
chihuahua	Hen	GER	S	M	5	ambi	20	**0°**	**x**
yorkshire terrier	Bri	GER	S	F	10	ambi	20	**31°**	**x**

Size: L = large, M = medium, S = small, Sex: F = female, M = male, Age is given in years, laterality: ambi-, left- or right-lateral, n = number of test series (in each test series 4 trials were performed), μ = mean vector in ° at the first locality and, if tested, at the second (distant) locality; at each of those distant localities 36 test series were performed., x = the dog was not tested at the second locality. The column "subject" refers to the first three letters of the respective dog's name. See the supporting information (S1 Table) for further detail.

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was either standing behind the dog, and had no eye contact with it, in the Czech Republic (Fig 1), or had dark sun glasses and stood on the opposing side of the dishes, facing the dog, in Germany.

All the dog owners were informed about the study, consented with the set-up and use of their dog(s) and were present at trials. The owners in the Czech Republic were coauthors of this study, their colleagues, and friends; the dog owners in Germany were approached via dog-training clubs.

Only the direction of the first choice was recorded. The dog was allowed to visit and take the snack also from the other dish. Apart from the chosen first direction in a given combination, the sequence of tested combinations within the trial, the dog's and owner's identities, locality, place, date, daytime, weather (sunny, cloudy, overcast, rainy), wind strength and direction were recorded. (However, no tests were performed on windy days.)

From the recorded choices, preferences for either left or right turn were calculated for all test combinations (N-E, E-S, S-W, W-N) within each trial, and the sum for all trials for each dog. Index of laterality was then calculated for each dog according to the formula (R–L) / (R + L) x

Fig 1. Photo illustrating the study setup.

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100, where R and L is the preference for using the right and left side, respectively [11]. Significance of lateralization was tested by chi-square test.

Independently, mean directional compass preference based on the frequency of first choices at a given locality in all pooled trials (at different day times, different days, different places within the locality) was calculated for each dog using circular statistics with Oriana 4.02 (Kovach Computing). Grand mean vectors were then calculated on the base of those mean dog/locality vectors for all the dogs, and subgroups with respect to laterality, breed, body size, sex, and age.

Results

Laterality

In dish-choice trials, altogether six dogs were identified as left-sided, five dogs as right-sided and 14 dogs were ambilateral based on the choices the respective dogs made in approaching one of the dishes placed left and right in front of them. There was no clear effect of breed and sex on laterality.

Compass preference

Testing the circular distribution of mean vectors of all dogs, as well as of dogs of a particular lateralization, body size, sex, and age revealed that there was an apparent preference for the north ("pull of the north") which was highly significant in small and medium-sized breeds but not in larger breeds, highly significant in females, in older dogs, in lateralized dogs but less significant or not significant in males, younger dogs, or ambilateral dogs (Table 2, Figs 2–5).

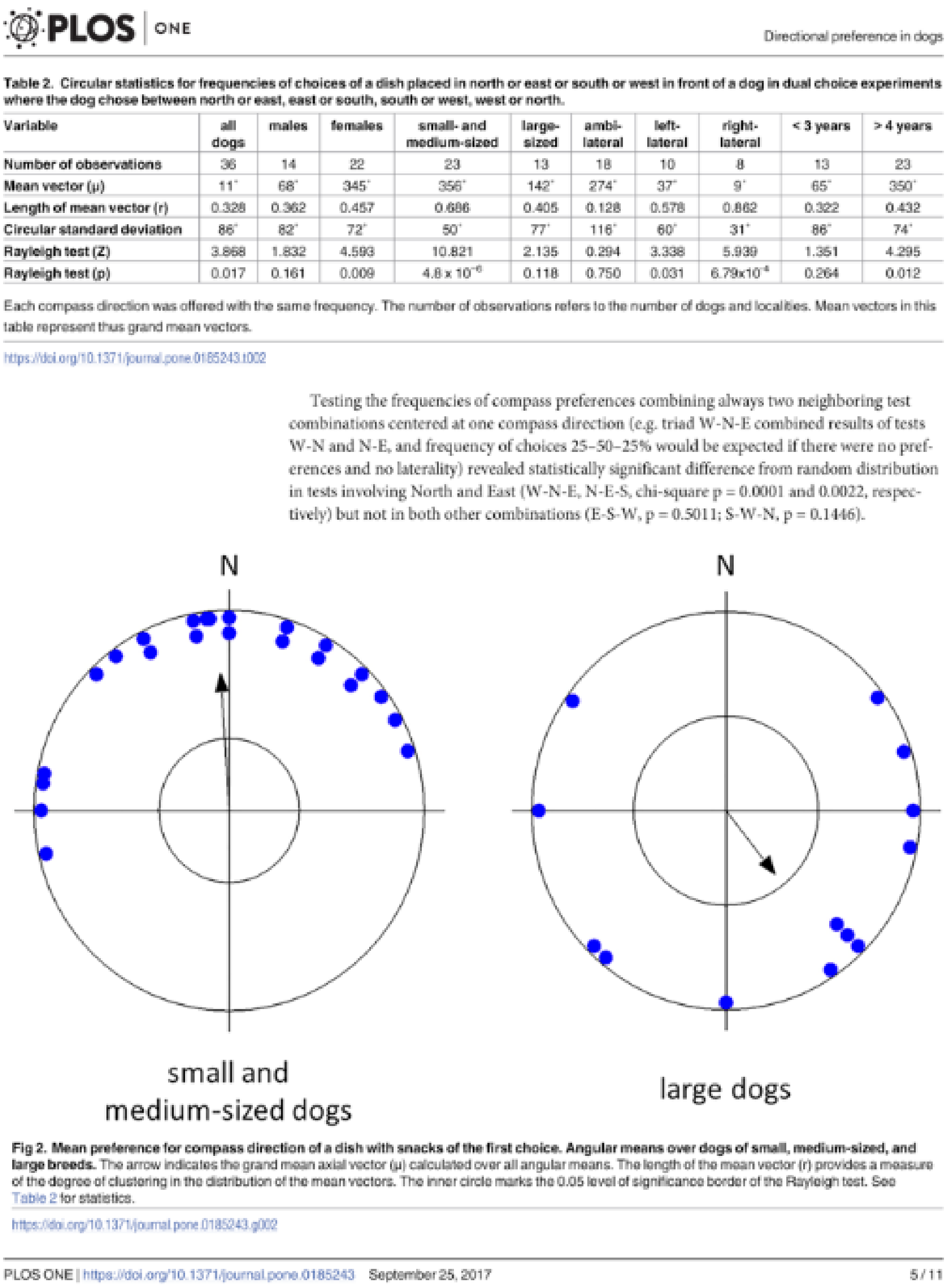

Table 2. Circular statistics for frequencies of choices of a dish placed in north or east or south or west in front of a dog in dual choice experiments where the dog chose between north or east, east or south, south or west, west or north.

Variable	all dogs	males	females	small- and medium-sized	large-sized	ambi-lateral	left-lateral	right-lateral	< 3 years	> 4 years
Number of observations	36	14	22	23	13	18	10	8	13	23
Mean vector (μ)	11°	68°	345°	356°	142°	274°	37°	9°	65°	350°
Length of mean vector (r)	0.328	0.362	0.457	0.686	0.405	0.128	0.578	0.862	0.322	0.432
Circular standard deviation	86°	82°	72°	50°	77°	116°	60°	31°	86°	74°
Rayleigh test (Z)	3.868	1.832	4.593	10.821	2.135	0.294	3.338	5.939	1.351	4.295
Rayleigh test (p)	0.017	0.161	0.009	4.8×10^{-6}	0.118	0.750	0.031	6.79×10^{-4}	0.264	0.012

Each compass direction was offered with the same frequency. The number of observations refers to the number of dogs and localities. Mean vectors in this table represent thus grand mean vectors.

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Testing the frequencies of compass preferences combining always two neighboring test combinations centered at one compass direction (e.g. triad W-N-E combined results of tests W-N and N-E, and frequency of choices 25–50–25% would be expected if there were no preferences and no laterality) revealed statistically significant difference from random distribution in tests involving North and East (W-N-E, N-E-S, chi-square p = 0.0001 and 0.0022, respectively) but not in both other combinations (E-S-W, p = 0.5011; S-W-N, p = 0.1446).

Fig 2. Mean preference for compass direction of a dish with snacks of the first choice. Angular means over dogs of small, medium-sized, and large breeds. The arrow indicates the grand mean axial vector (μ) calculated over all angular means. The length of the mean vector (r) provides a measure of the degree of clustering in the distribution of the mean vectors. The inner circle marks the 0.05 level of significance border of the Rayleigh test. See Table 2 for statistics.

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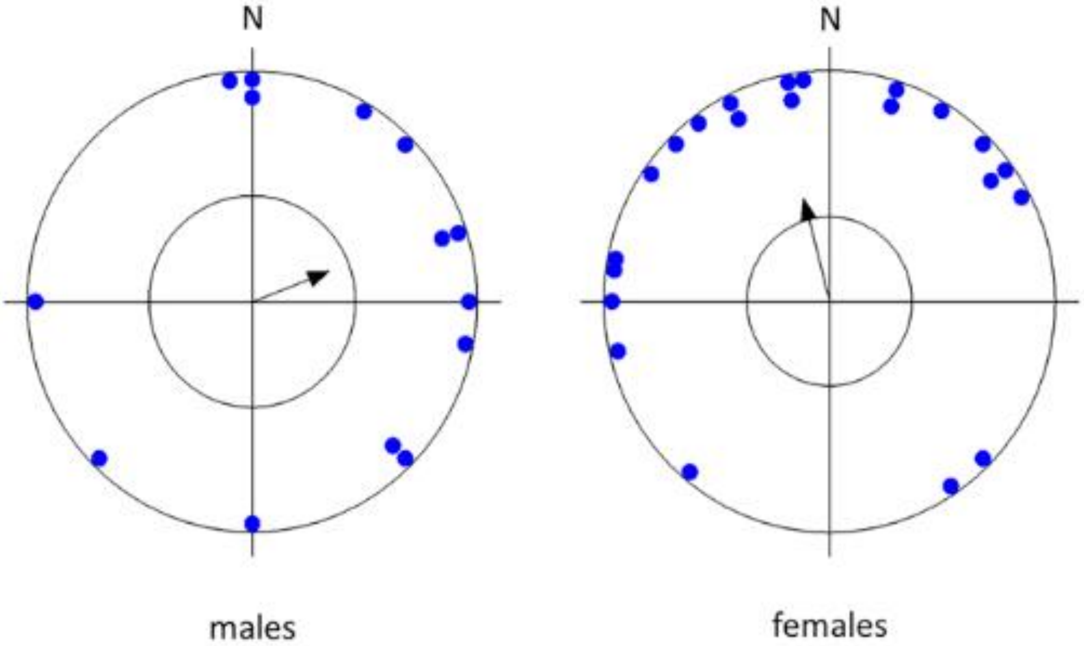

Fig 3. Mean preference for compass direction of a dish with snacks of the first choice. Angular means over males and females separately. The arrow indicates the grand mean axial vector (μ) calculated over all angular means. The length of the mean vector (r) provides a measure of the degree of clustering in the distribution of the mean vectors. The inner circle marks the 0.05 level of significance border of the Rayleigh test. See Table 2 for statistics.

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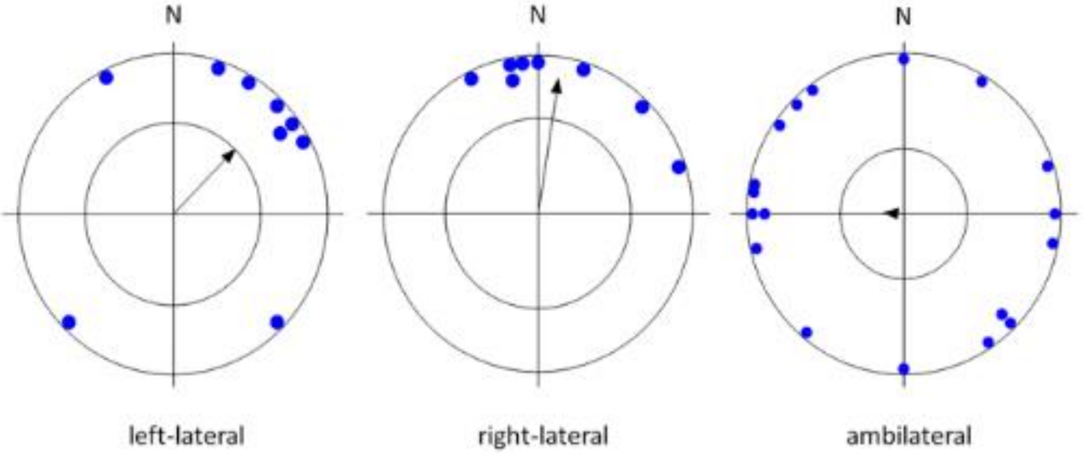

Fig 4. Mean preference for compass direction of a dish with snacks of the first choice. Angular means over dogs of different lateralization types. The arrow indicates the grand mean axial vector (μ) calculated over all angular means. The length of the mean vector (r) provides a measure of the degree of clustering in the distribution of the mean vectors. The inner circle marks the 0.05 level of significance border of the Rayleigh test. See Table 2 for statistics.

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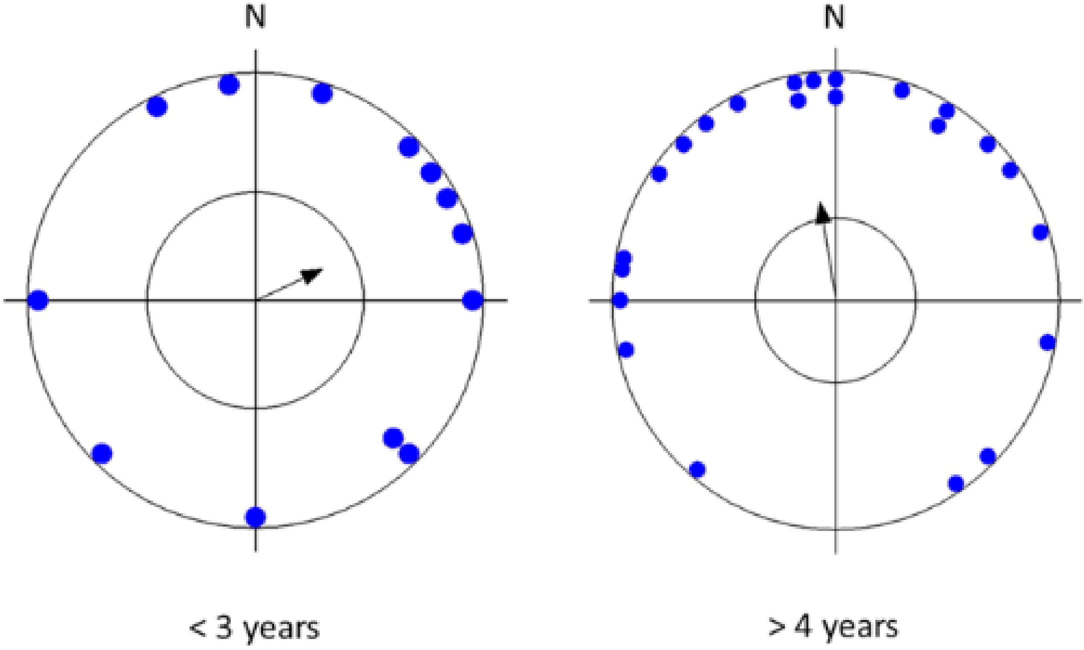

Fig 5. Mean preference for compass direction of a dish with snacks of the first choice. Angular means over dogs of different age categories. The arrow indicates the grand mean axial vector (μ) calculated over all angular means. The length of the mean vector (r) provides a measure of the degree of clustering in the distribution of the mean vectors. The inner circle marks the 0.05 level of significance border of the Rayleigh test. See Table 2 for statistics.

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Discussion

We tested the preference of dogs to choose between two dishes with snacks that were placed left and right, in different compass directions (north and east, east and south, south and west or west and north) in front of them. Some dogs were right-lateral, some left-lateral but most of them were ambilateral. There was a preference for the dish placed north compared to the one placed east of the dog ("pull of the north"). This effect was significant in small and medium-sized breeds but not in larger breeds, significant in females, in older dogs, in lateralized dogs but not significant in males, younger dogs, or ambilateral dogs. None of the extrinsic factors which might have influenced the directional choice, but the Earth's magnetic field, was stable in space and time. All other factors (possible hints from the owners, landmarks, sun position, weather, homing direction) were stochastically changing and could not have systematically influenced the observed "pull of the north".

His master's voice?

The test was performed by several different dog owners. We do not see any possibility how the dogs might have been systematically (i.e. in one common direction and only in a compass combination involving north and east) influenced in their decision by their owners. The dogs had no eye contact with their owners. In fact, every choice was rewarded, and the dogs were allowed to take also the reward from the second dish, so that effective learning, e.g. on some landmark in the surroundings, was not possible. Besides that, the next trial occurred at another place, or site or even at another locality, at another day, another day-time, and the sequence of tested compass direction pairs changed.

Effect of sun?

"Pull of the north" could be theoretically explained as avoidance of blinding sun. This explanation is rather anthropomorphic and does not consider the fact that dogs are lower than human and that the dishes were placed on the ground. Moreover, this argument would be valid only in the choice test "north x east" on sunny mornings in spring and autumn when sun is low. Analogously, however, preference for the north would be expected also in the choice test "north x west" in the evening on sunny days. Furthermore, dogs would be expected to avoid south during midday on sunny days. Larger (higher) dogs are expected to be more prone to blinding than smaller (lower) dogs. Apart from the fact that actually there was never a choice test "north x south" or "east x west" where sun avoidance could be actually realized, none of these possible explanations for the results was supported. Circular analysis of the tests performed in "lateral" dogs in the morning (grand mean vector $\mu = 42^\circ$, $r = 0.510$, $SD = 66$, Rayleigh test $p = 0.041$, $N = 12$) and in the afternoon (grand mean vector $\mu = 22^\circ$, $r = 0.650$, $SD = 53$, Rayleigh test $p = 0.0006$, $N = 16$) revealed no differences (99% confidence interval for μ a.m. 343°-100°, for p.m. 347°-57°). Also "ambilateral" dogs displayed no differences between morning and afternoon choices (morning: $\mu = 286^\circ$, $p = 0161$, $N = 12$; afternoon = 269°, $p = 0.488$, $N = 15$). There were no significant differences between whatever combination of directions (N x W, N x E, S x E, S x W) tested in the morning and in the afternoon, respectively.

Note also that in Central Europe, Czech Rep. and Germany, where the experiments were done, the sun hours make on average only about 35% of the light hours—so, if the experiments are randomly and evenly distributed throughout the year and daytimes, the probability of being blinded by the sun (if one lifts the head or the sun is low and one looks into it), is 35%. The probability that one actually has problems to recognize where on the sky the sun stands is 65%. Note also that according to the hitherto knowledge dogs do not perceive polarized light.

Other possible effects?

The Earth's magnetic field parameters in both countries are comparable. The declination in Essen (Germany) is 1.5°, the declination in Prague (Czech Rep.) is 3.5°, and the difference is thus only 2°. The dogs had to decide, however, for one of the two directions which were 90° apart. Most importantly, directions in the field in both countries were measured by means of a compass which shows *always* a direction to the magnetic pole, i.e. not by means of a geographical map which would show direction to the geographic pole.

Although in Germany relatively more larger dogs were represented in the sample than in the Czech Republic, there was no apparent country bias if smaller versus larger, lateral versus ambilateral, etc. dogs in the two countries, were compared. In spite of the large dataset, the subgroups (breeds, age, sex, lateralization) were still rather small and heterogeneous and did not enable us to reliably test which of those facts was most decisive. We have also no idea why larger breeds "failed" in the compass test. It should be noticed that this category was composed mainly of (labrador) retrievers but it would be preliminary to claim that this breed is ambilateral and/or "magnet-blind". The fact that older dogs oriented more towards the north than younger dogs might correlate with their experience and established orientation strategies.

We have purposely performed the experiments outdoors because the magnetic field in buildings might be disturbed and because dogs tested indoors might orient with respect to geometry of rooms. Since it cannot be excluded that dogs might orient with respect to landmarks also outdoors, care was taken when selecting the testing place that its surroundings were free of any landmarks within the radius of at least 30 m, a condition which could not be complied with indoors.

Conclusions and prospects

The here presented two-dish choice test widens the range of tests reviewed in [12, 24] suitable for assessment of lateralization in dogs. At the same time it shows that laterality plays a role not only in intrinsic kinesthetic reactions but also in directional goal-oriented decisions. Moreover there is an apparent "pull of the north", which is particularly strong in the test combination "north—east". Laterality and "pull of the north" are thus phenomena which should be considered in diverse tasks (and behavioral tests) with which dogs or other animals might be confronted. On the other hand, the phenomenon of laterality should be likewise considered in studies of spatial orientation and navigation. The interaction and possible conflict between lateralization and "pull of the north" might be also considered as a reason for shifted magnetic alignment observed in different animal species in different contexts [9]. It might prove to be significant for understanding the putative (and thus far unknown) mechanism of magnetoreception that the field observations and laboratory experiments in diverse animal species consistently show a shift of directional preference from north or south to the east after a treatment with a strong magnetic pulse e.g. [25–26]. Moreover, roe deer were found to prefer to escape northwards but to avoid escaping eastwards [27]. These (and further own unpublished) observations indicate some sensory interaction between perceiving north and east directions.

Supporting information

S1 Table. Information on tested dogs, particulars of trials and their results. Age is given in years, the choice for a dish in the respective combination in compass degrees.
(XLSX)

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8.2 Příloha č. 2

Turning preference in dogs: north attracts while south repels

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ABSTRACT

It was shown earlier that dogs, when selecting between two dishes with snacks placed in front of them, left and right, prefer to turn either clockwise or counterclockwise or randomly in either direction. This preference (or non-preference) is individually consistent in all trials but it is biased in favor of north if they choose between dishes positioned north and east or north and west, a phenomenon denoted as "pull of the north". Here, we replicated these experiments indoors, in magnetic coils, under natural magnetic field and under magnetic field shifted 90° clockwise. We demonstrate that "pull of the north" was present also in an environment without any outdoor cues and that the magnetic (and not topographic) north exerted the effect. The detailed analysis shows that the phenomenon involves also "repulsion of the south". The clockwise turning preference in the right-preferring dogs is more pronounced in the S-E combination, while the counterclockwise turning preference in the left-preferring dogs is pronounced in the S-W combination. In this way, south-placed dishes are less frequently chosen than would be expected, while the north-placed dishes are apparently more preferred. Turning preference did not correlate with the motoric paw laterality (Kong test). Given that the choice of a dish is visually guided, we postulate that the turning preference was determined by the dominant eye, so that a dominant right eye resulted in clockwise, and a dominant left eye in counterclockwise turning. Assuming further that magnetoreception in canines is based on the radical-pair mechanism, a "conflict of interests" may be expected, if the dominant eye guides turning away from north, yet the contralateral eye "sees the north", which generally acts attractive, provoking body alignment along the north-south axis.

Introduction

Dogs in two-choice experiments, when selecting between two dishes with snacks placed in front of them, 90° apart, left and right, prefer to turn either clockwise ("right-preferring") or counterclockwise ("left-preferring") or randomly in either direction ("irresolute"). This turning preference (or non-preference) is individually consistent in all trials but it is biased in favor of north if they choose between dishes positioned north and east or north and west, a phenomenon we denoted as "pull of the north" [1]. This phenomenon was particularly pronounced in older dogs, females, smaller and medium-sized breeds, dogs exhibiting a turning preference, and especially in the north-east choice. We suggested that “pull of the north” represents a further indication of magnetoreception in dogs, the other being non-random directional alignment during marking [2], which was, however, significantly changed when exposed to bar magnets [3], the ability to find a bar magnet [4], or the existence of the so-called "compass run" exhibited during homing [5].

We are, however, aware that for the ultimate evidence of magnetoreception, experiments in defined manipulated magnetic field and/or under conditions of disturbed magnetoreception are necessary. Moreover, the proximate reason for “pull of the north” remains unclear and should be at least hypothesized.

Laterality, i.e. a predictable, non-random preference for using one side of the body (limbs, brain hemisphere, sensory organs) spontaneously or if forced or restricted to choose between two sides, is a known phenomenon in humans and animals. Laterality may be inborn, imprinted, or entrained and has to be taken into account in maze and behavioral two-choice animal experiments [6-10].

Laterality in dogs has been intensively studied with regard to the motoric (efferent) aspect (paw laterality, Kong-test: [11-15]; sensory (afferent) aspect [16-18]; cognitive [19], and emotional aspects [20-22]. Interestingly, and contrary to studies in humans, turning (directional, rotational) preference has remained understudied.

Most people are right-handed, yet tend to instinctively veer to the left upon entering a new space [23]. Interestingly, the counterclockwise action goes also for most athletic tracks, horse and car races, and for baseball players running the bases [24]. There is even evidence that the chariot races at ancient Rome's Circus Maximus ran counterclockwise, too [25-26]. So, in sports, where competitors enter the field of play from the outside of a traced circle, a right-directional choice would lead to a counter-clockwise motion. But when entering the field of action from within the circle - walking out of your apartment to take the dog for a walk, and encountering intersections - right directional choices would tend towards tracing a clockwise path [23]. Interestingly, in the countries, where people drive on the left side of the road, retail shoppers tend to turn counterclockwise - when navigating store aisles, while in the countries, where people drive and keep on sidewalks right, veer clockwise [23]. Tendencies of people to turn either direction are known to architects who use them to design shopping galleries to funnel shoppers in the wished direction [23].

While the preference to turn in a certain direction can be explained by individual inborn laterality (handedness) and experience (facilitation), or – e.g. in the context of our experiment of choice between two dishes, which is a visually guided task, through visual laterality - the "pull of north" is expected to have a magnetoreceptive ground. Examination of this phenomenon has a heuristic potential in getting insight into the very seat and mechanism of magnetoreception, which still remain enigmatic [27].

Sensory laterality (or asymmetry) has been described also in the context of spatial orientation in general and magnetoreception in particular. It has been found that homing pigeons rely more on the right olfactory system in processing the olfactory information needed for the operation of the navigational map [28]. An earlier study [29] has shown that the magnetic compass of a migratory bird, the European robin (*Erithacus rubecula*), was lateralized in favour of the right eye/left brain hemisphere. However, it has been later demonstrated [30] that the described lateralization is not present from the beginning, but develops only as the birds grow older. In another study [31], it was shown that pigeons can perceive and process magnetic compass directions with the right eye and left brain hemisphere as well as the left eye and right brain hemisphere. However, while the right brain hemisphere tended to confuse the learned direction with its opposite (axial response), the left brain hemisphere specifically preferred the correct direction (angular response). The findings thus demonstrated bilateral processing of magnetic information, but also suggested qualitative differences in how the left and the right brain deal with magnetic cues.

Based on the hitherto knowledge and the above arguments,

1) We hypothesize that if "pull of the north" is due to magnetoreception (and indeed no other explanation is apparent), it should be demonstrated also in an artificial magnetic field shifted by magnetic coils, i.e. the artificially shifted magnetic North should exert the same effect as the natural geomagnetic North.
2) We expect that, consistently with results of the previous study [1] "pull of the north" is more pronounced in "lateralized" dogs and more in the North-East (N-E) combination than in the North-West (N-W) choice.

Furthermore, following questions can be raised (and should be tested) to get insight into the nature of the turning preference:

3) Does the directional preference for turning correlate with motoric laterality (such as paw-laterality, i.e. "handedness")?
4) Is pull of the north a) symmetrical (bilateral, i.e. of the same strength in the clockwise as in counterclockwise direction), or b) asymmetrical (unilateral, i.e. stronger in one particular direction)?

Material and methods

Ethics statement

The study did not involve any disturbance or discomfort to the study subjects. The Professional Ethics Commission of the Czech University of Life Sciences in Prague has decided that according to the law and national and international rules, this study has not a character of an animal experiment and does not require a special permit.

Subjects

Altogether, 23 domestic dogs *Canis familiaris* (11 M, 12 F) from six breeds with pedigree and an average age of 4.8 (± 2.8) years (Table 1) were used in this study. The dogs were pets living in households. All the dog owners were present with their dogs at trials.

Table 1. List of the tested dogs and resulting indices of directional preference.

Dog	Owner	Breed	Sex	Age	Paw motorical laterality	Initial turning preference	Mean turning preference
Amalka	KB	Dachshund D	F	5	51	17	46
Arthur	ES	Dachshund N	M	2	n.m.	-32	-45
Azizi	JS	Beagle	M	6	6	-4	19
Barca	LS	Fox Terrier	F	12	0	67	42
Bertik	KB	Dachshund D	M	6	8	-29	-48
Bessy	JA	Fox Terrier	F	8	26	22	42
Figy	KB	Dachshund D	F	5	9	-4	8
Gofi	JA	Fox Terrier	F	3	-70	-95	-96
Hard	JA	Fox Terrier	M	2	-46	22	2
Hugo	KB	Dachshund D	M	3	n.m.	-25	-17
Hurvinek	KB	Dachshund D	M	7	51	-46	-45
Jimmy	ES	Dachshund N	M	2	n.m.	60	35
Kacka	KB	Dachshund D	F	5	25	-17	-18
Kuky	KB	Dachshund D	M	7	27	50	40
Naty	ES	Münsterländer	M	3	n.m.	-45	-62
Offi	JS	Beagle	F	9	-3	8	6
Pecka	KB	Dachshund D	F	2	-44	17	29

Plysak	KB	Dachshund D	F	2	10	-37	-60
Punta	KB	Dachshund D	M	3	-1	-8	-34
Roxxy	JS	Beagle	F	9	100	62	67
Shedy	ES	Weimaraner	M	5	n.m.	27	40
Sisi	KB	Dachshund D	F	3	n.m.	12	42
Zofka	KB	Dachshund D	F	2	-20	54	46

Paw motoric laterality = laterality index based on the Kong test; Initial turning preference Turning preference index in the first trials of each dog. Mean turning preference = = mean turning preference index over all trials of each dog. Sex: F = female, M = male. Age is given in years. Dachshund N = normal-sized dachshund, Dachshund D = dwarf-sized dachshund, n.m. = not measured.

Experimental equipment

The experiment took place in a magnetic coil at the field research station Truba, Kostelec nad Černými lesy, (N 50°0.40480', E 14°50.11145'), a detached workplace of the Faculty of Forestry and Wood Sciences, Czech University of Life Sciences in Prague, Czech Republic. The magnetic coil (a Merritt coil, built according Kirschvink [32]) is 4 x 4 x 4 m and is located in a separate special building. It is shielded from radiofrequency waves. It is controlled from a separate building next to the coil building. The magnetic field in coils is manipulated by a MagFieldG control software through a GMP4 RJ4.01 control unit and three current amplifiers, each for the Bx axis, the By axis and the Bz axis. The generation system for GMP4 3D coil system is used to create a defined direct and slowly changing magnetic field and it serves to drive the coil system to create a defined magnetic field.

Magnetic induction values in the Cartesian coordinate system (axis Bx = -3225 nT; axis By = 17800 nT; axis Bz = 45448 nT) were set for the experiment, thereby rotating the magnetic field by 90 ° magnetic North was shifted to the topographic (= geomagnetic) East. The magnetic field strength and inclination were maintained as for geomagnetic values for local geographic conditions. The magnetic coil space was used also for the control experiment to test the dogs under local geomagnetic conditions, while other experimental conditions were preserved identic, i.e. shielding of radiofrequency waves, avoiding other influences (wind, sun, outside sounds). The coil room was equipped with cameras (AXIS P5624-E 50HZ - PTZ IP camera, TD / N, 18x zoom, HD 720p, IP66, PoE +) for video recording of the entire experimental space, network speaker with SIP, PoE support (AXIS C3003-E NETWORK HORN SPEAKER, Double - sided audio) and microphone (AXIS T8353A MICROPHONE 3.5MM) at the control station to secure communication of the leading experimenter in the control workplace with two experimenters in the coil.

Experimental procedure

Dogs were tested indoors, in a room housing the magnetic coils, and should make the choice between two identical dishes. The dishes were placed at a distance of 2.9 m from the point of release of the dog, always a plus and minus 30° from the starting point. Both dishes contained the same treats and dogs were always allowed to empty both. After placing the dishes, the dog was ready for the starting point and waited to obtain a permit to go to a dish. The dogs could not see the placement of the reward dishes. Three experimenters were involved in the experiment; two were present in the magnetic coil (the owner was guarding the dog and prohibited it from seeing the preparation procedure, and the other was preparing the placement of the rewarded dishes), the third experimenter was in the control room using a microphone and headsets to communicate with the two other colleagues, changed the experimental magnetic conditions (switching between control and experimental conditions) according to a randomized schedule and recorded the results (direction of dog first choice) (Fig 1). Note that this person was the only one who knew the actual position of the magnetic North inside the coil.

Fig 1. Experimental setup as monitored from above by a camera placed at the ceiling of the room, showing the sequence from release of the dog (A) to its choice of one of two dishes (D).

Each dog was tested in three to five test series under the control conditions with the magnetic North (mN) being 0°, and in the same number of test series in an artificially shifted magnetic field with mN=90° (where magnetic north was set on topographic east). The order of the test series (control first, shifted field second or shifted field first, control second) was taken into account. Tests series were performed at different days, at different daytimes, evenly distributed over the whole day.

Because a series included four trials in each dish combination alignment (i.e. N-E, E-S, S-W, and W-N), individual dogs experienced either 48 or 80 trials (in 12 or 20 complete series) in which their turning preference (first dish choice) was recorded under control conditions and the same number of records was gathered for experiments in the shifted magnetic field. The difference in the number of series and trials experienced by individual dogs was given by their availability for our study.

In addition, the dog's identity, date, time, sequence of trials combinations, and the order of the trials in the respective series were recorded.

Paw preferences

To determine paw preference (motoric laterality of dogs), a modified Kong test [e.g. 12, 16, 33] was used. In this test, it is recorded with which paw (left or right) the dog holds a Kong, a dog toy (KONG Company) when trying to get the food stuffed inside. A plastic yoghurt cup was used instead of Kong. The inner walls and bottom of the cup were covered with a dog's delicacy such as lard, cream cheese. Each dog was tested at home in an open area for 10 minutes while the dog played with the cup and tried to lick it out and the number of touches with either paw was recorded. Simultaneous touches with both paws were also recorded but were not included in the calculation of the index of laterality. The dogs who did not touch the cup during test of paw preference were excluded from the analysis of the Kong test.

Data analyses

From the recorded choices for each dog, in each trial, the left and right turning preferences were summed, for all four combinations (W-N; N-E; E-S; S-W) separately. For data analysis, the **turning preference index** was calculated in tests performed in the control and shifted magnetic field. The formula (R-L / R + L) x 100 was used, where the R=right and L=left sides are the total numbers of the first choice of left or right dishes. The **laterality index** for the paw preference (Kong test) was calculated using the same formula. The value of the index can range from -100 to -25 (= left-pawed dog) to 25 - 100 (= right-pawed dog). Dogs with index values between -24 and 24 were considered ambilateral. For the turning preference, altogether ten indices (LI) were calculated; one for each dish combination alignment (N-E, E-S, S-W, and W-N), i.e. four altogether in the control conditions and four altogether in the shifted magnetic field conditions. Furthermore, we calculated one mean index for control conditions and one mean index for shifted magnetic field (Table S1). The dogs were divided in turning preference left-preferring, right-preferring or irresolute (ambilateral) preference according to

[33] based on results of the first trials (Initial turning preference in Table 1). Generalized Linear Model (GLM) contained the interaction between Magnetic field and Turning preference classes.

From the recorded choices, preferences for either left or right turn were calculated for all test combinations (N-E, E-S, S-W, W-N) within each trial, and the sum of all trials of each dog. Index of directional preference was then calculated (according to the above formula) for each dog.

All data were analyzed using the SAS System (SAS, version 9.4). For calculating Spearman correlation coefficient we used PROC CORR. To analyze the factors affecting the directional preference index (dependent variable) we used a multivariate Generalized Linear Mixed Model (GLM, PROC MIXED). We constructed two GLMs. The models were applied as a fixed-effect models designed for the repeated measures, i.e., in SAS, with REPEATED = order of testing and the SUBJECT = Name of the dog with compound symmetric covariance structures for repeated measures (TYPE=cs). The first GLM was constructed with the predicted fixed factors Magnetic coil in an interaction with the Turning preference classes, and then we added other variables listed in Table S2 in case they could affect the directional preference index. None of these variables appeared significant and therefore we will not mention them in the text any more. Least squares means (LSMEANs) were calculated for the categorical fixed effects by computing the mean of each treatment and averaging the treatment means. These means of means were then used to compare the factors.

The second model was designed to estimate repeatability of the directional preference across experimental conditions. The GLM contained the only fixed factor Magnetic coil. We calculated repeatability as the intraclass correlation coefficient [34] by adding the RCORR option to the REPEATED.

Independently, mean directional compass preference based on the frequency of first choices in a given combination in all pooled trials was calculated for each dog using circular statistics with Oriana 4.02 (Kovach Computing). Grand mean vectors were then calculated on the base of those mean dog vectors for all the dogs, and subgroups with respect to turning preference, experimental condition, sex, and age.

Results

Paw preference (motoric laterality, Kong test)

Following the a priori set criterion, out of altogether 17 dogs tested, 3 dogs were classified as left-lateral, 6 as right-lateral, and 8 as irresolute (ambi-lateral) (Table 1). There was no apparent effect of sex, age, breed or owner on this type of laterality. The correlation between the Kong and overall turning preference tests was rather weak (r_s=0.317, P=0.22).

Turning preference under the control (mN=0°) and experimental (mN=90°) conditions

Following the a priori set criterion, out of altogether 23 dogs tested, 6 dogs were classified as clockwise-preferring (right-lateral), 7 dogs as counterclockwise-preferring (left-lateral), and 10 as irresolute (ambi-lateral) (Table 1). There was no significant difference in turning preferences of individual dogs between control conditions (mN=0°) and the shifted magnetic field conditions (mN=90°) (Fig 2). There was a variation in the turning preference index according to the magnetic north direction and Turning preference classes ($F_{(23, 131)}$=4.59, P<0.0001, Figs 2-3). For the dogs with clockwise turning preference, there was a trend towards increasing the turning preference index from NE, SE, SW and NW. In other words, the clockwise turning dogs exhibited the lowest turning preference index in the combination North-East. However, only the difference between NE vs NW and between NE and SW, and only in the shifted magnetic field, reached the level of significance (P=0.05) (Fig. 2 left). For the dogs with counterclockwise turning preference, the most intensive counterclockwise preference was shown in SE orientation in comparison with NW and partly NE, while the weakest preference was in shown in the NW combination. Significant differences were achieved in the shifted magnetic field in SE vs NW, and under control conditions in NE vs SE, SE vs NW, SW vs NW (Fig 2, middle). No trend nor differences were detected for dogs showing irresolute turning preference (Fig. 2, right).

Fig 2. Turning preference index (Least Square Means ± SE) for clockwise-preferring (left), counterclockwise-preferring (middle), and irresolute (right) dogs under the conditions of the magnetic North (mN)=0° (control) and mN=90° (shifted magnetic field) for the four particular combinations of the placement of dishes.

Fig 3. Numbers in each quadrant (in the respective four compass combinations: N-E, E-S, S-W, W-N) show **Mean values of turning preference indices** calculated from individual dogs and pooled across all trials (both control and shifted magnetic field conditions). Data were partitioned by turning preference (left figure shows clockwise turning preference, right figure shows counterclockwise turning preference; irresolute dogs were not calculated. The green arrow over the dog's head in the centre of the circle indicates the direction of view of the (supposedly) dominant eye which guides turning direction, while the red arrow shows the direction of view of the contralateral eye, supposed to exert "pull of the north" if heading northwards. Green arrow outside the circle designates the preferred direction of turning, the shorter red arrow designates "pull of the north".

There was significant bias from the overall turning preferences in the eastern hemisphere, expressed as the "pull of the north", in that a dish placed eastwards was more frequently chosen than a dish placed southwards and a dish placed northwards more frequently than a dish placed eastwards, resulting in an average (theoretical) preference for NNE (Fig 4, Table 2). In a more differentiated view, this result was due to a dominant preference of females and/or clockwise preferring dogs for North (over East) and to an additional weaker pull of the East over South in males and/or counterclockwise preferring dogs. "Pull of the north" in irresolute dogs was indicated but not significant (Table 2, Figs 2-3).

Fig 4 Mean preference for compass direction of a dish with snacks of the first choice. Angular means over dogs preferring to turn clockwise, those preferring to turn counterclockwise, dogs which were irresolute in their preference, and over all dogs. The arrow indicates the grand mean axial vector (μ) calculated over all angular means. The length of the mean vector (r) provides a measure of the degree of clustering in the distribution of the mean vectors. The inner circle marks the 0.05 level of significance border of the Rayleigh test. See Table 2 for statistics.

Table 2. Circular statistics for frequencies of choices of a dish placed in different cardinal compass directions in front of a dog in dual choice experiments, where the dog chose between north or east, east or south, south or west, west or north.

Variable	All trials	mN=0°	mN=90°	1st series	2nd series
Number of dogs tested	23	23	23	23	23
Mean vector (μ)	21°	43°	350°	22°	17°

Length of mean vector (r)	0.485	0.557	0.464	0.347	0.566
Circular standard deviation	69°	622°	71°	83°	61°
95% Confidence interval (-/+) for μ	349°-53°	16°-70°	316°-23°	335°-68°	351°-44°
99% Confidence interval (-/+) for μ	339°-63°	7°-78°	305°-34°	321°-82°	342°-52°
Rayleigh test (Z)	5.402	7.134	4.945	2.766	7.378
Rayleigh test (p)	0.004	4.92E-04	0.006	0.061	3.68E-04

Variable	males	females	clockwise preferring	counterclockwise preferring	irresolute
Number of dogs tested	11	12	6	7	10
Mean vector (μ)	44°	0°	6°	48°	3°
Length of mean vector (r)	0.517	0.529	0.637	0.655	0.356
Circular standard deviation	66°	65°	54°	53°	82°
95% Confidence interval (-/+) for μ	358°-90°	318°-42°	318°-53°	9°-90°	279°-87°
99% Confidence interval (-/+) for μ	344°-105°	304°-56°	303°-68°	354°-103°	252°-113°
Rayleigh test (Z)	2.939	3.357	2.431	3.005	1.268
Rayleigh test (p)	0.049	0.031	0.084	0.043	0.288

Each compass direction was offered with the same frequency. Mean vectors in this table represent thus grand mean vectors. Cf. Fig 4.

Repeatability of turning preference

A single factor of Magnetic coil was not significant ($F_{1, 22} = 1.16$, $P=0.86$). On the other hand, Repeatability was high ($r=0.76$).

Discussion

Turning preference did not correlate with the motoric paw laterality (Kong test). Apparently, both types of preferences are controlled by different proximate mechanisms / pathways. This conclusion is consistent with earlier findings [35] showing that visual (sensory) and paw (motoric) laterality in dogs are independent of each other. None of the dogs had any previous experience with emptying cups (i.e. Kong-type tests). None of the dogs used in this study had a history of being trained "Heel" to come and follow the master at her/his left (or right) side. Consequently, their turning preferences can be considered natural, spontaneous, inborne, and not entrained. Accordingly, there was no significant difference in the turning preference in particular dogs between the first and second experimental series and there was no effect of the respective owner. Interestingly, among the dogs who turned clockwise there were more females, while among the dogs turning counterclockwise there were more males. The sample was, however, too small to allow any general conclusion with regard to the effect of sex on turning preference. In fact, no clear effect of sex on turning preference was found in a previous study (with a different composition of the study sample) [1].

Consistently with results, of the previous study in open field [1], the turning preference was consistent for each particular dog for all combinations of placement of dishes also in an interior with uniform walls, no apparent landmarks, and no sun or wind cues. Concordantly with the results of the previous study, this preference was slightly, yet significantly disturbed (or pronounced) in that the north-placed dishes were more frequently chosen than would be expected according to the average turning preference of each particular dog. Most important in the context of the present study is the finding that, magnetic and not topographic, north affected the mentioned bias.

The detailed analysis shows, however, that the "pull of the north" is a more complex phenomenon, involving also "repulsion of the south". These effects are unilateral: the clockwise turning preference in the right-preferring dogs is more pronounced ("accelerated") in the S-E combination, while the counterclockwise turning preference in the left-preferring dogs is "accelerated" in the S-W combination. On the other hand, N-E combination decreases ("decelerates") clockwise turning preference in the right-preferring dogs, while in the N-W combination, the counterclockwise turning preference in the left-preferring dogs will be reduced. In this way, in the total, south-placed dishes are less frequently chosen than would be expected, while the north-placed dishes are apparently more preferred. Since "rotational deceleration" is stronger in N-E than the N-W combination, while the "acceleration" is stronger in the S-E than in the S-W combination, the resulting theoretical mean preference is for Northeast.

It may be of relevance and significance in this context that the analysis of published results on magnetic alignment behaviour in a variety of vertebrate species revealed that magnetic alignment typically coincides with the north-south magnetic axis, however, the mean directional preferences of an individual or group of organisms is often rotated clockwise from the north-south axis [36-38]. The deviation from the magnetic north-south axis could originate at different levels in the sensory hierarchy: it could be related either to asymmetries at the sensor level or to functional brain asymmetries, i.e. central processing.

Although the mode of the perception of the magnetic compass direction in animals remains enigmatic [27], findings from behavioral, histological, neuroanatomical, and electrophysiological studies have led to several physically viable theoretical models that might also apply to dogs. Two mechanisms are most widely discussed in the literature: the magnetite-based mechanism and the radical-pair mechanism.

Perhaps the most intuitively appealing mechanism to explain magnetosensitivity in animals is the idea of a small permanent magnet inside the animal that acts like a compass needle [39]. Magnetite-based sensors may be located anywhere in the body, they do not need to be concentrated in (paired) organs and they can be very tiny.

Another proposed mechanism for magnetoreception in animals is based on an effect of the magnetic field on the quantum spin states of a photo-excited chemical reaction that forms long-lived, spin correlated radical pair intermediates (radical pair mechanism; [40-41]. It is believed to occur in the specialized retinal cells [42-43]. It is assumed that the magnetic field may generate a “visual” pattern of varying light intensity, color, and/or contrast superimposed on the normal visual scene [40, 44-45]. The model suggests that north or south “patterns” are more clearly recognizable and easier to be followed than east or west “patterns”. Accordingly, and alternatively, the “pull of the north” could be also interpreted as a “deflection / repellence by the east or west”.

Given that the choice of a dish in our experiment was visually guided, we may postulate that the turning preference was determined by the dominant eye, so that a dominant right eye resulted in clockwise, and a dominant left eye in counterclockwise turning. Assuming further that magnetoreception in canines is based on the radical-pair mechanism [46-47], a "conflict of interests" may be expected, if the dominant eye guides turning away from north, yet the contralateral eye "sees the north", which generally acts attractive, provoking body alignment along the north-south axis. To test this hypothesis, visual dominance (eyedness) in particular dogs should be studied in an independent test, e.g. sensory jump test [35].

Magnetic alignment might have an adaptive function in that it provides a global reference frame that helps to structure and organize spatial behavior and perception over many different spatial scales. For example, one possibility is that magnetic alignment helps to put the animal into register with a known orientation of a mental (cognitive) map, reducing the complexity of local and long-distance navigation, and reduces the demands on spatial memory [44]. This would be analogous to strategies used in human orientation; it is much simpler and intuitive to navigate when the navigators align themselves with a physical map (i.e. the users rotate their body direction to coincide with the alignment of the physical map), rather than to navigate by mentally rotating the physical map to align with the user's orientation. Therefore, we suggested that the mental map in animals is fixed in alignment with respect to the magnetic field [2, 38]. Indeed, important component(s) of the cognitive map may be derived from the magnetic field (see below) and spontaneous magnetic alignment behavior may help to place the animal into register with this map. This relatively simple alignment strategy would help animals to reliably and accurately 'read' their cognitive map and/or extend the range of their maps when exploring unfamiliar environments. Accordingly, animals of different taxa were frequently reported to prefer to head about northwards when feeding (reviewed in [36-38]).

We suggest that the described simple turning test has a high heuristic potential and should be extended for tests of visual laterality and be performed under a wider array of experimental conditions to get more insight into the very mechanism, seat and function of magnetoreception.

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Supplementary Materials:

S1 Table. Indices of laterality each tested dog. ITP = index of turning preference; W-N designates the combination in which the test dishes were placed west and north; N-E= designates the combination in which the test dishes were placed north and east; E-S designates the combination in which the test dishes were placed east and south; S-W= designates the combination in which the test dishes were placed south and west, mN=0° designates a control experiment; mN=90° designates an experimental condition with a shifted magnet field.

S2 Table. Variables available for statistical analysis.

S3 Table. Source data.

Figure 1

Click here to access/download;Figure;Figure 1.jpg

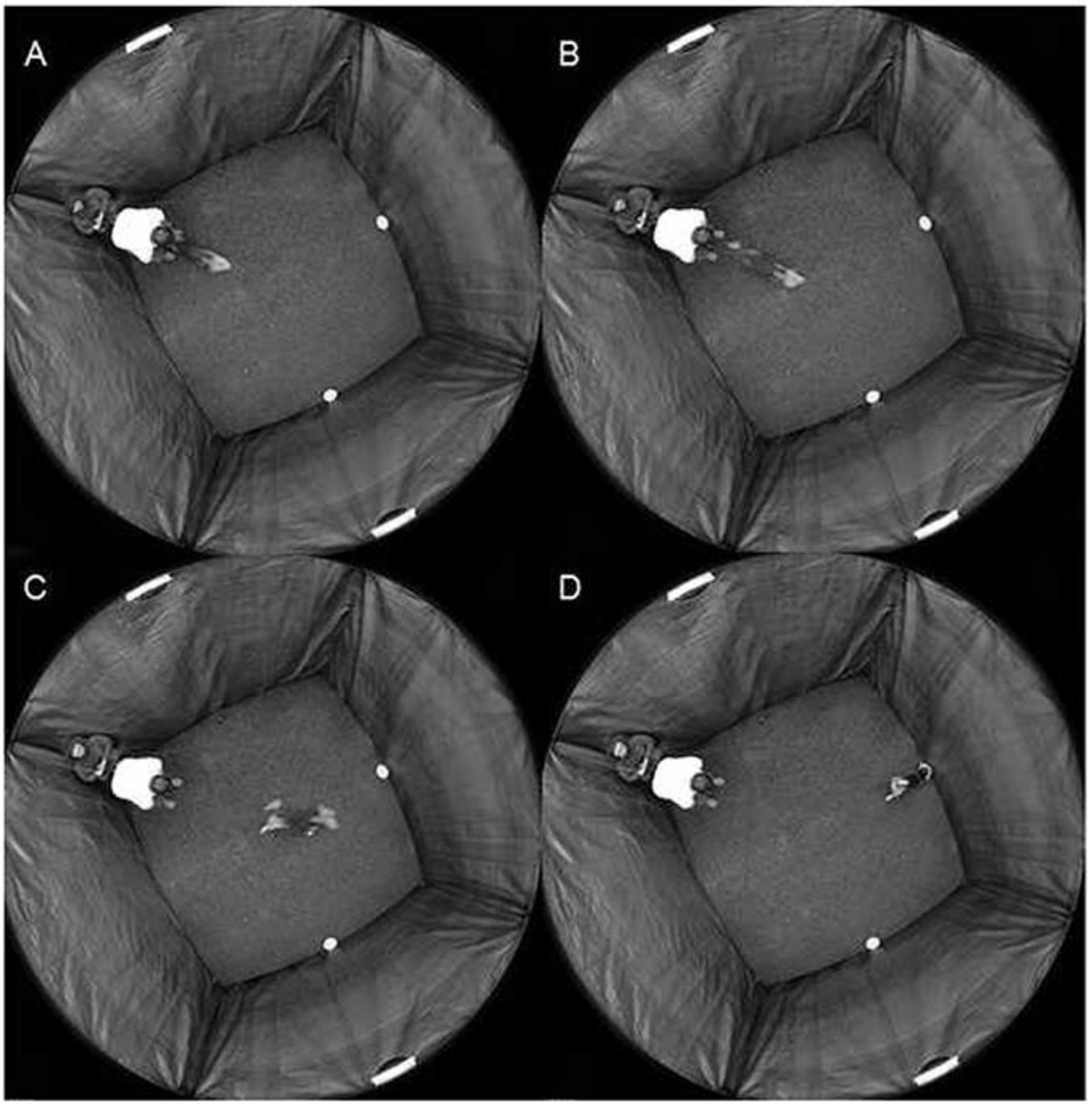


Figure 2

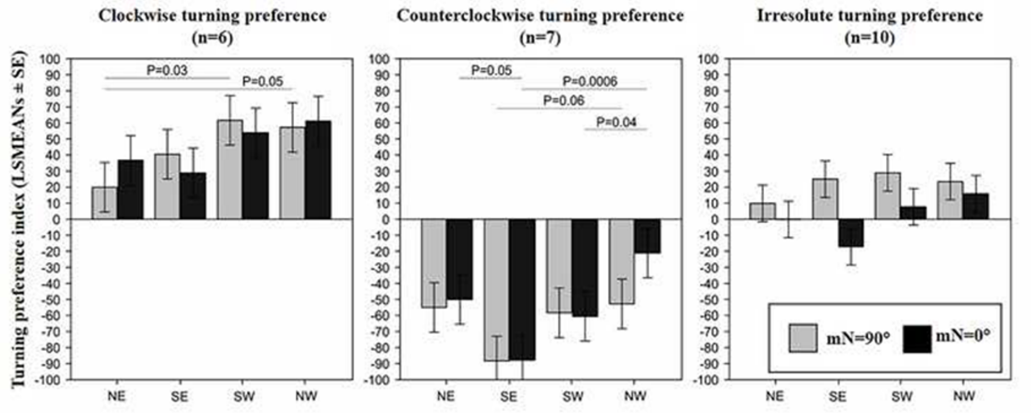
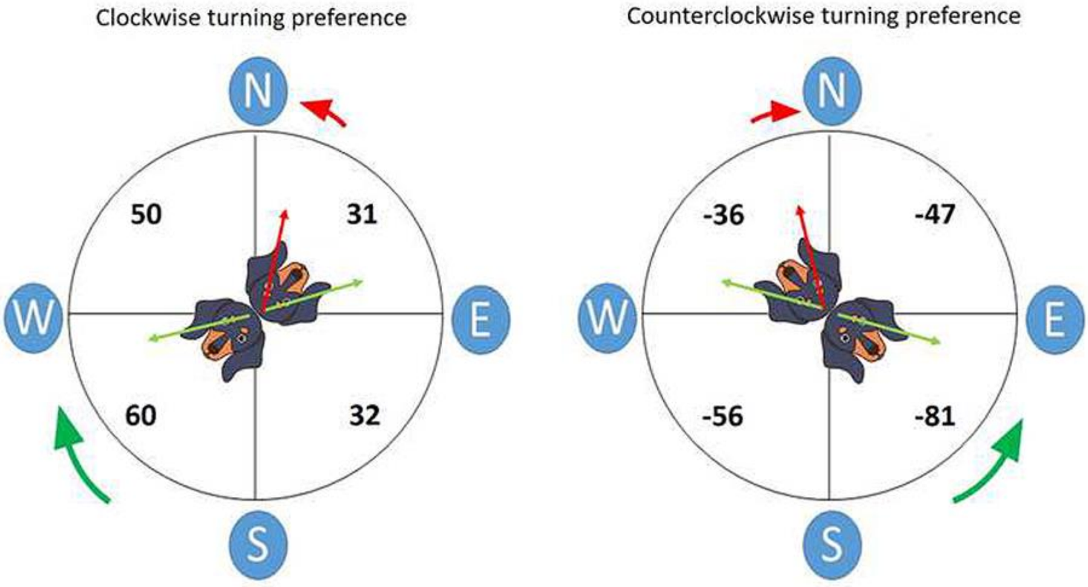
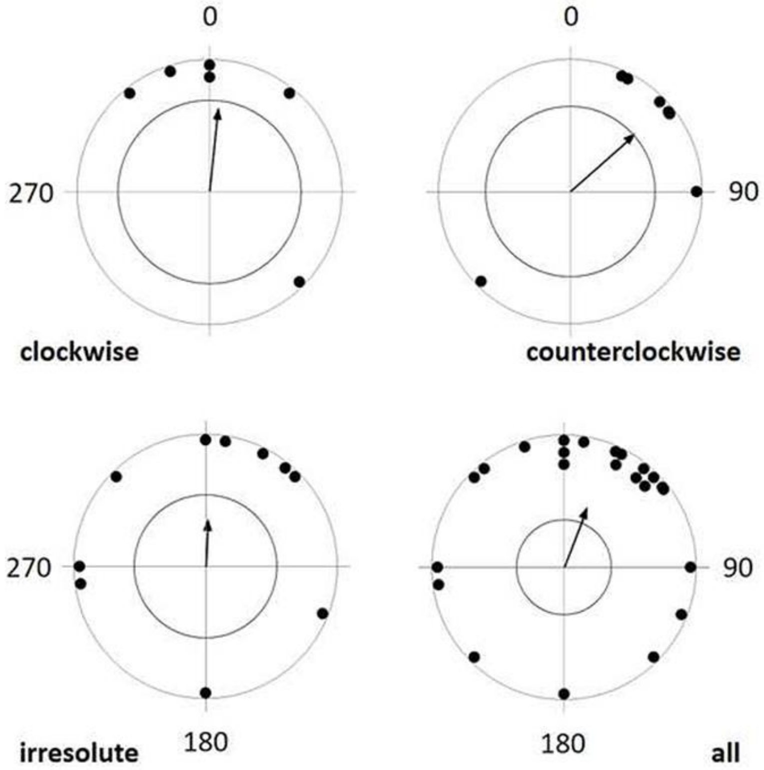


Figure 3




0
0
270
90
clockwise
counterclockwise
270
90
irresolute
180
180
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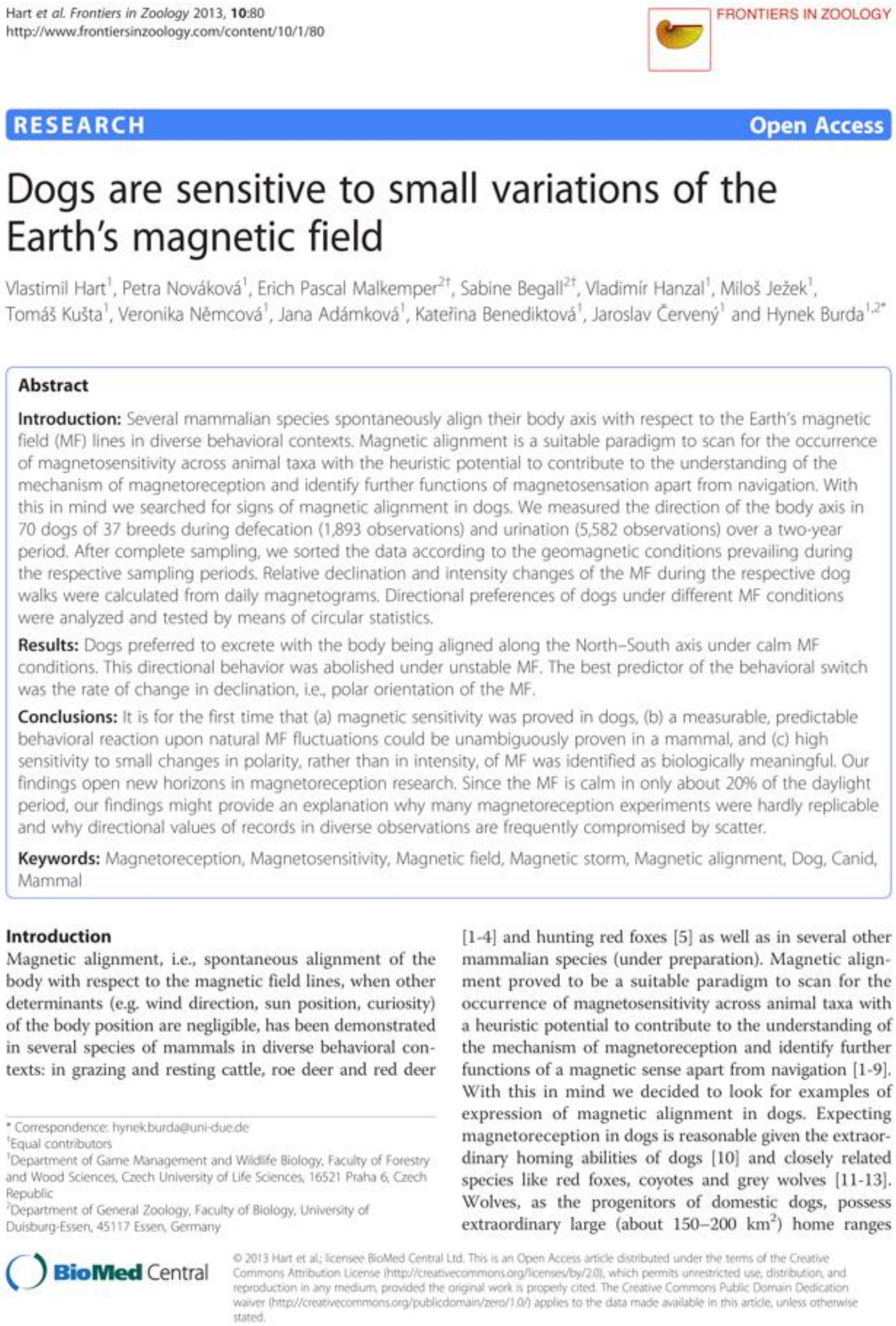
8.3 Příloha č. 3



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Dogs are sensitive to small variations of the Earth's magnetic field

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Abstract

Introduction: Several mammalian species spontaneously align their body axis with respect to the Earth's magnetic field (MF) lines in diverse behavioral contexts. Magnetic alignment is a suitable paradigm to scan for the occurrence of magnetosensitivity across animal taxa with the heuristic potential to contribute to the understanding of the mechanism of magnetoreception and identify further functions of magnetosensation apart from navigation. With this in mind we searched for signs of magnetic alignment in dogs. We measured the direction of the body axis in 70 dogs of 37 breeds during defecation (1,893 observations) and urination (5,582 observations) over a two-year period. After complete sampling, we sorted the data according to the geomagnetic conditions prevailing during the respective sampling periods. Relative declination and intensity changes of the MF during the respective dog walks were calculated from daily magnetograms. Directional preferences of dogs under different MF conditions were analyzed and tested by means of circular statistics.

Results: Dogs preferred to excrete with the body being aligned along the North–South axis under calm MF conditions. This directional behavior was abolished under unstable MF. The best predictor of the behavioral switch was the rate of change in declination, i.e., polar orientation of the MF.

Conclusions: It is for the first time that (a) magnetic sensitivity was proved in dogs, (b) a measurable, predictable behavioral reaction upon natural MF fluctuations could be unambiguously proven in a mammal, and (c) high sensitivity to small changes in polarity, rather than in intensity, of MF was identified as biologically meaningful. Our findings open new horizons in magnetoreception research. Since the MF is calm in only about 20% of the daylight period, our findings might provide an explanation why many magnetoreception experiments were hardly replicable and why directional values of records in diverse observations are frequently compromised by scatter.

Keywords: Magnetoreception, Magnetosensitivity, Magnetic field, Magnetic storm, Magnetic alignment, Dog, Canid, Mammal

Introduction

Magnetic alignment, i.e., spontaneous alignment of the body with respect to the magnetic field lines, when other determinants (e.g. wind direction, sun position, curiosity) of the body position are negligible, has been demonstrated in several species of mammals in diverse behavioral contexts: in grazing and resting cattle, roe deer and red deer [1-4] and hunting red foxes [5] as well as in several other mammalian species (under preparation). Magnetic alignment proved to be a suitable paradigm to scan for the occurrence of magnetosensitivity across animal taxa with a heuristic potential to contribute to the understanding of the mechanism of magnetoreception and identify further functions of a magnetic sense apart from navigation [1-9]. With this in mind we decided to look for examples of expression of magnetic alignment in dogs. Expecting magnetoreception in dogs is reasonable given the extraordinary homing abilities of dogs [10] and closely related species like red foxes, coyotes and grey wolves [11-13]. Wolves, as the progenitors of domestic dogs, possess extraordinary large (about 150–200 km^2) home ranges

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[14], suggesting superior orientation abilities. Furthermore, strong indications for magnetosensation in the red fox [5] add on to the growing evidence.

A discovery of magnetoreception in dogs would open totally new horizons for magnetobiological research: Dogs are widely available experimental subjects all over the world and can easily be trained to react on diverse sensory stimuli [15]. In addition, as dogs are still readily used as experimental animals in a wide array of biomedical applications [16], the discovery of a new sense would have far reaching consequences also in this sector.

Having been inspired by our hitherto observations in other animals [1-3,5-8,17], we monitored spontaneous alignment in dogs during diverse activities (resting, feeding and excreting) and eventually focused on excreting (defecation and urination incl. marking) as this activity appeared to be most promising with regard to obtaining large sets of data independent of time and space, and at the same time it seems to be least prone to be affected by the surroundings.

Results

Circular analysis of the distribution of all values of all dogs irrespective of the magnetic field conditions revealed significant but highly scattered axial orientation during defecation (Table 1). This orientation was, however, not confirmed by the grand mean vector (calculated over the dogs' mean values, Figure 1, Table 1). Since no significant differences between males and females and since no angular preferences during defecation were found (not shown here), we only present the axial analyses combined for both sexes here.

After the data were sorted according to the magnetic field conditions (specifically, Kp-index, relative changes of magnetic field intensity or of declination) at the time

Table 1 Analysis of body orientation during defecation (all records, i.e., no differentiation between different magnetic conditions)

Variable	Defecation: all records			
	Pooled	Pooled	Means (n > 5)	Means (n > 5)
Data type	angular	axial	angular	axial
Number of observations	1,893	1,893	49	49
Mean vector (μ)	133°	157°/337°	80°	148°/328°
Length of mean vector (r)	0.013	0.052	0.043	0.209
Circular standard deviation	169°	70°	144°	51°
95% Confidence interval (−/+) for μ	-	-	-	121°-174°
99% Confidence interval (−/+) for μ	-	-	-	112°-183°
Rayleigh test (Z)	0.307	5.203	0.091	2.143
Rayleigh test (p)	0.736	0.006	0.914	0.117

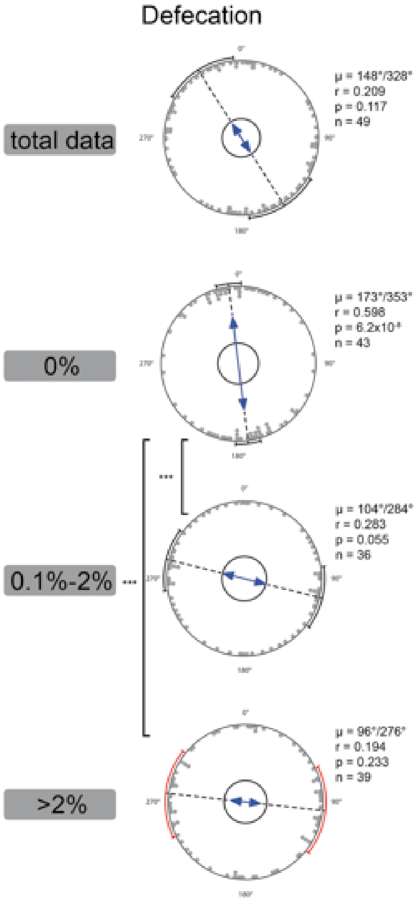

Figure 1 Analysis of dog body alignment during defecation. Axial analysis of mean vectors of dogs with more than 5 observations. Total data and observations from three different categories of relative changes of the declination of the Earth's magnetic field are shown from top to bottom (0%, 0.1-2%, >2%). Each pair of opposite dots indicates the axis of the mean vector of all observations of a single dog. The direction (μ) and length (r) of the (grand) mean vector and the p-value of the Rayleigh uniformity test as well as the sample size are given next to each diagram. μ and r are indicated by the direction and length of the blue arrows, respectively. Small inner circles indicate the 5%-significance level of the Rayleigh test. Circle segments at the outer circle represent the 95%-confidence intervals (red circle segments indicate intervals that could not be calculated with confidence due to large circular standard deviations). Statistically significant differences between the distributions according to the Mardia-Watson-Wheeler test are indicated by asterisks (*** = $p < 0.001$). A significant N-S axial orientation (i.e., 95%-confidence interval includes the N-S axis) can only be seen under conditions of zero declination change. See Tables 1–2 for further details on statistics.

Table 2 Axial analysis of alignment during defecation in all dogs (pooled data or mean vectors of particular dogs sorted into three categories according to the rate of changes of magnetic field declination)

	Pooled raw data			Means per dog (n > 5)		
Declination rate	**0%**	**0.1-2%**	**>2%**	**0%**	**0.1-2%**	**>2%**
Number of observations	607	542	744	43	36	39
Mean vector (μ)	176°/356°	111°/291°	109°/289°	173°/353°	104°/184°	96°/276°
Length of mean vector (r)	0.216	0.106	0.03	0.598	0.283	0.194
Circular standard deviation	50°	61°	76°	29°	45°	52°
95% Confidence interval (−/+) for μ	168°-183°	-	-	164°-182°	81°-127°	-
99% Confidence interval (−/+) for μ	166°-185°	-	-	161°-185°	74°-134°	-
Rayleigh test (Z)	28.248	6.133	0.672	15.353	2.891	1.464
Rayleigh test (p)	$<10^{-12}$	0.002	0.511	$6.20 \cdot 10^{-8}$	0.055	0.233

of recording, a differentiated picture emerged. The relative declination change proved to be the best predictor of alignment, i.e.,. sorting the data according to this parameter provided the most significant results. Analysis of pooled recordings as well as of mean vectors of recordings in dogs sampled during calm magnetic field conditions (relative change in declination = 0%; minimum of 5 observations per dog) revealed a highly significant axial preference for North–South alignment during defecation (for 0% declination change: μ = 173°/353° ± 9° (mean vector orientation angle; 95% confidence interval), r = 0.598 (mean vector length), Rayleigh test: n = 43, $p = 6.2 \cdot 10^{-8}$, Z = 15.353; second order (weighted) statistics: weighted mean vector (WMV): 175°/355°, r = 0.253, Hotelling test: n = 43, $p = 1.02 \cdot 10^{-7}$, F = 24.463; Tables 2 and 3, Figures 1 and 2). With increasing relative declination changes the distribution of dogs' body orientations became more scattered and in the category "> 2%" the distribution was random, and no directional preference was apparent (Table 2, Figure 1). The distributions of dogs' body orientations in the intervals of relative declination change "0.1%-2%" as well as "> 2%" were significantly different from the distribution at 0%, both, when pooled raw data and when means per dog were analyzed (Mardia-Watson-Wheeler test, p < 0.001, Figure 1). The same dependence of the directional preference on the relative changes of the magnetic declination appeared when males and females were treated separately (not shown here).

Analysis of the alignment during defecation under conditions of stable magnetic declination (0% changes) revealed no significant effect of sex. There may be a slight effect of age: dogs in the age category 2.5-7 years showed a clearer preference than younger or elder dogs (not shown). The effect of the dog breed could not be tested because of small sample sizes.

Circular analysis of the distribution of the pooled raw data demonstrated a significant deviation from random distribution also in urinating dogs (Table 4). Analyzing

Table 3 Alignment during defecation in dogs (females and males) in two-hour periods

Variable	All records 20:01–08:00	Quiet MF 20:01–08:00	All records 08:01–12:00	Quiet MF 08:01–12:00	All records 12:01–16:00	Quiet MF 12:01–16:00	All records 16:01–20:00	Quiet MF 16:01–20:00
Number of observations	442	173	599	188	396	109	455	144
Mean vector (μ)	157°/337°	177°/357°	152°/332°	178°/358°	12°/192°	170°/350°	147°/327°	173°/353°
Length of mean vector (r)	0.042	0.239	0.073	0.2	0.074	0.26	0.088	0.176
Circular standard deviation	72°	48°	65°	51°	65°	47°	63°	53°
95% Confidence interval (−/+) for μ	112°-202°	165°-190°	130°-174°	163°-192°	345°-39°	155°-184°	126°-168°	155°-192°
99% Confidence interval (−/+) for μ	98°-217°	161°-193°	123°-181°	159°-106°	337°-48°	151°-189°	119°-175°	149°-198°
Rayleigh test (Z)	0.769	9.866	3.17	7.533	2.145	7.367	3.54	4.474
Rayleigh test (p)	0.463	0.000052	0.042	0.000535	0.117	0.000632	0.029	0.011

Columns denoted "quiet MF (magnetic field)" give statistic values based on analysis of those data from the respective column "all values" which were collected under conditions of stable declination (0% change). Due to small sample sizes for single dogs, the data of all observations done in the given period are pooled. Pooling is justified in this case because samples for respective dogs have comparable sizes and because males and females show comparable posture and alignment during defecation. The data were not sorted here according to months but the distribution of observations during respective months of the year is comparable, so that the distribution of the data (and resulting analysis) would not change if winter and summer observations were further separated. Note random circular distribution of the alignment when all data for respective time periods are analyzed, but highly significant preference for the North–South axis when only observations made under quiet magnetic field are considered.

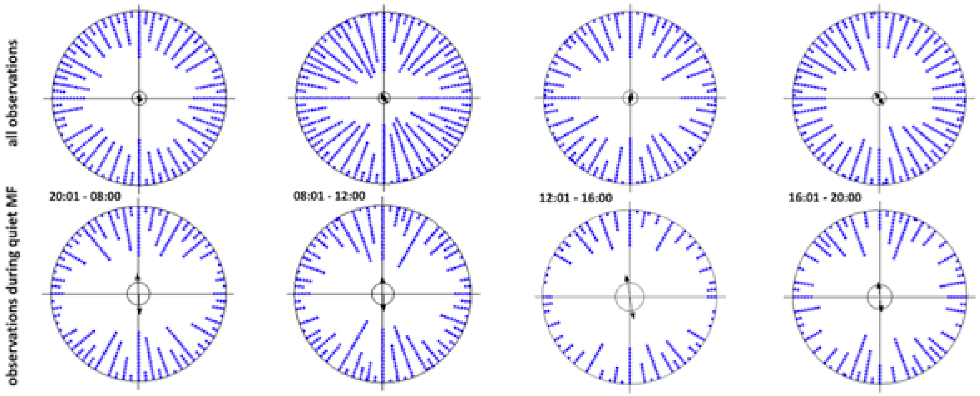

Figure 2 Alignment during defecation in dogs (females and males) in different day periods. Columns denoted "quiet MF (magnetic field)" give statistic values based on analysis of those data from the respective column "all values" which were collected under conditions of stable declination (0% change). Due to small sample sizes for single dogs, the data of all observations done in the given period are pooled. Pooling is justified in this case because samples for respective dogs have comparable sizes and because males and females show comparable posture and alignment during defecation. The data were not sorted here according to months but the distribution of observations during respective months of the year is comparable, so that the distribution of the data (and resulting analysis) would not change if winter and summer observations were further separated. Note random circular distribution of the alignment when all data for respective time periods are analyzed, but highly significant preference for the North–South axis when only observations made under quiet magnetic field are considered.

this data for males and females separately we found a slight difference in the patterns between sexes: Pooled data (without the dog M07) and mean values of all males with at least 5 observations revealed a significant angular preference for North-West heading during urination (Table 5). The male borzoi M07 contributed approximately one third of the urination data and was analyzed separately (Table 6); the results were similar to the pooled data of all other males. In contrast, females showed an axial preference for approximately the North–South axis during urination (Table 7). As in the case of defecation, sorting the data according to the relative changes of declination revealed a significant effect of this factor and a significant axial North–South alignment only under calm MF conditions (for 0% declination change: $\mu = 167°/347° \pm 16°$, $r = 0.343$, Rayleigh test: $n = 49$, $p = 0.003$, $Z = 5.766$; second order (weighted) statistics: WMV: 173°/353°, $r = 0.165$, Hotelling test: $n = 49$, $p = 5.08 \cdot 10^{-4}$, $F = 8.952$; Figure 3, Tables 5, 6, 7). The raw data distributions during changing declination were significantly different from the

Table 4 Angular and axial analysis of body orientation in dogs during urination

Data type	Urination: (all records)									
	Angular					Axial				
	Pooled			Means (n ≥ 5)		Pooled			Means (n ≥ 5)	
	Males	M07	Females	Males	Females	Males	M07	Females	Males	Females
Number of observations	1,402	2,478	1,702	24	35	1,402	2,478	1,702	24	35
Mean vector (μ)	312°	298°	13°	292°	331°	154°/334°	175°/355°	5°/185°	89°/269°	11°/191°
Length of mean vector (r)	0.048	0.105	0.03	0.213	0.213	0.037	0.196	0.132	0.101	0.292
Circular standard deviation	141°	122°	152°	101°	101°	74°	52°	58°	61°	45°
95% Confidence interval (−/+) for μ	268°-356°	283°-313°	309°-78°	217°-8°	269°-34°	125°-183°	171°-179°	358°-12°	9°-169°	348°-33°
99% Confidence interval (−/+) for μ	254°-10°	278°-318°	288°-98°	193°-31°	249°-53°	116°-192°	169°-180°	356°-15°	343°-194°	341°-40°
Rayleigh test (Z)	3.215	27.075	1.517	1.088	1.584	1.875	94.735	29.524	0.246	2.99
Rayleigh test (p)	0.04	$1.74 \cdot 10^{-12}$	0.219	0.341	0.206	0.153	$< 10^{-12}$	$< 10^{-12}$	0.786	0.049
Rao's spacing test (U)	307.618	354.479	339.271	140.383	131.675	325.078	357.094	346.675	134.75	145.847
Rao's spacing test (p)	<0.01	<0.01	<0.01	>0.1	>0.1	<0.01	<0.01	<0.01	>0.1	>0.1

Data for the male dog M07 are presented in a separate column due to large sample size.

Table 5 Angular analysis of alignment during urination in all males (pooled data without dog M07 and mean vectors of all males sorted into three categories according to the relative changes of magnetic field declination)

	Pooled raw data			Means per dog (n ≥ 5)		
Declination rate	**0%**	**0.1-2%**	**>2%**	**0%**	**0.1-2%**	**>2%**
Number of observations	491	256	655	22	15	22
Mean vector (μ)	293°	12°	84°	291°	355°	195°
Length of mean vector (r)	0.129	0.08	0.006	0.367	0.349	0.07°
Circular standard deviation	116°	129°	182°	81°	83°	132°
95% Conf. interval (−/+) for μ	265°-321°	310°-74°	-	246°-335°	290°-61°	315°-76°
99% Conf. interval (−/+) for μ	256°-329°	290°-94°	-	232°-349°	270°-81°	239°-151°
Rayleigh test (Z)	8.17	1.619	0.028	2.959	1.828	0.109
Rayleigh test (p)	$2.83 \cdot 10^{-4}$	0.198	0.973	0.05	0.162	0.899
Rao's spacing test (U)	260.285	281.656	283.053	148.258	147.139	127.188
Rao's spacing test (p)	<0.01	<0.01	<0.01	>0.1	>0.1	>0.5

distribution under calm magnetic conditions (Mardia-Watson-Wheeler test, $p < 0.05$, Figure 3).

Discussion

Dogs rely much on their owner, and for many tasks they might anticipate the demanded behavior by reading their owner's facial expression and make use of unintentional experimenter-given cues [18-20]. This adds a bias-trap to any research relying on behavioral studies and particularly conditioning. However, this is certainly not a confounder in our study because the dogs do not have to fulfill a certain task, but perform everyday routine behavior.

The study was truly blind. Although the observers were acquainted with our previous studies on magnetic alignment in animals and could have consciously or unconsciously biased the results, no one, not even the coordinators of the study, hypothesized that expression of alignment could have been affected by the geomagnetic situation, and particularly by such subtle changes of the magnetic declination. The idea leading to the discovery of the correlation emerged after sampling was closed and the first statistical analyses (with rather negative results, cf. Figure 1) had been performed. Also, the acquisition of data on magnetic declination was carried out without knowledge of heading values on the respective time and date.

Table 6 Angular analysis of alignment during urination in male borzoi (M07)

Declination rate	**0-1.7%**	**1.8-3.3%**	**≥3.4%**
Number of observations	957	818	703
Mean vector (μ)	310°	285°	280°
Length of mean vector (r)	0.154	0.08	0.078
Circular standard deviation	111°	129°	130°
95% Confidence interval (−/+) for μ	294°-327°	250°-320°	241°-318°
99% Confidence interval (−/+) for μ	289°-332°	240°-331°	229°-331°
Rayleigh test (Z)	22.64	5.18	5.517
Rayleigh test (p)	$1.47 \cdot 10^{-10}$	0.006	0.015
Rao's spacing test (U)	345.705	344.156	341.565
Rao's spacing test (p)	< 0.01	< 0.01	< 0.01

Data are sorted into three categories according to the *relative changes* of magnetic field declination. Limits of the categories were chosen so that sample sizes are comparable.

We found no differences in alignment of females and males during defecation and of females during urination, which might be related to a similar posture the animals are adopting during defecation (in all dogs) and urination (in females). Urinating males have a slightly different preference to orient their body axis than urinating females (cf. Figure 3); this could be caused by leg lifting during urination in males. Indications of different directional tendencies depending on which leg (left or right) is lifted are currently under study. All recordings were made outside on open fields, and routes of walks were routinely changed to exclude or limit pseudoreplications which would arise when dogs are defecating or urinating at just a few places within their kennel or house yard.

Natural fluctuations of the Earth's magnetic field [21,22] have previously been suggested to disturb orientation in birds [23-25], bees [26] and whales [27]; and even to affect vegetative functions and behavior in humans [28,29], reviewed also in [22].

In this study, we provide the first clear and simply measurable evidence for influence of geomagnetic field variations on mammal behavior. Furthermore, it is the first demonstration of the effect of the shift of declination, which has to our knowledge never been investigated before. Previous studies of the effect focused mainly on the variations in field intensity. Although intensity and declination changes are mostly concomitant, declination change was a better predictor of dog alignment. Interestingly, the rate and direction of the changes disturb more effectively

Table 7 Axial analysis of alignment during urination in all females (pooled data and mean vectors of particular dogs sorted into three categories according to the relative changes of magnetic field declination)

	Pooled raw data			Means per dog (n ≥ 5)		
Declination rate	**0%**	**0.1-2%**	**>2%**	**0%**	**0.1-2%**	**>2%**
Number of observations	603	396	703	27	20	29
Mean vector (μ)	5°/185°	2°/182°	11°/191°	0°/180°	7°/187°	23°/203°
Length of mean vector (r)	0.208	0.131	0.068	0.434	0.159	0.134
Circular standard deviation	51°	58°	66°	37°	55°	57°
95% Conf. interval (−/+) for μ	357°-12°	347°-17°	349°-33°	163°-196°	312°-63°	328°-78°
99% Conf. interval (−/+) for μ	354°-15°	342°-22°	342°-40°	157°-201°	294°-80°	311°-95°
Rayleigh test (Z)	26.146	6.839	3.251	5.085	0.503	0.52
Rayleigh test (p)	$4.41 \cdot 10^{-12}$	0.001	0.039	0.005	0.61	0.598
Rao's spacing test (U)	312.836	330	339.004	156.975	135.002	129.554
Rao's spacing test (p)	<0.01	<0.01	<0.01	>0.05	>0.1	>0.5

than absolute values. Here, for the first time the response can be attributed to the rate of magnetic field changes.

Typically, the daily declination comprises westward-shifts in the morning and eastward-shifts in the afternoon, while the magnetic field is rather stable at night [21,22]. This calls for necessity to test whether the dog alignment is not actually influenced primarily by time of the day and most probably by position of the sun on the sky. We can, however, exclude this alternative. First, days when the magnetic field parameters change erratically and unpredictably (i.e., magnetic storms) are quite frequent. These changes have been well studied by others and are described in the literature (cf. [21,22] for reviews). Second, the data collection was not biased to either morning or afternoon (Table 8). Third, periods of sampling under conditions of quiet magnetic field were rather evenly distributed in the course of the day. Fourth, and most importantly, alignment during excreting was apparent under conditions of quiet magnet field, irrespective of the time of day or month. Time of day per se was not a reliable predictor of expression of alignment (Figure 2, Tables 3, 9). Fifth, generally, there are on average 1,450 sunshine hours per year at maximum in the Czech Republic and in Germany, on localities where measurements were done. Even if we would assume that these sunshine hours were evenly distributed over the daylight period and the year (as our observations were), there would only be a probability of 33% that the

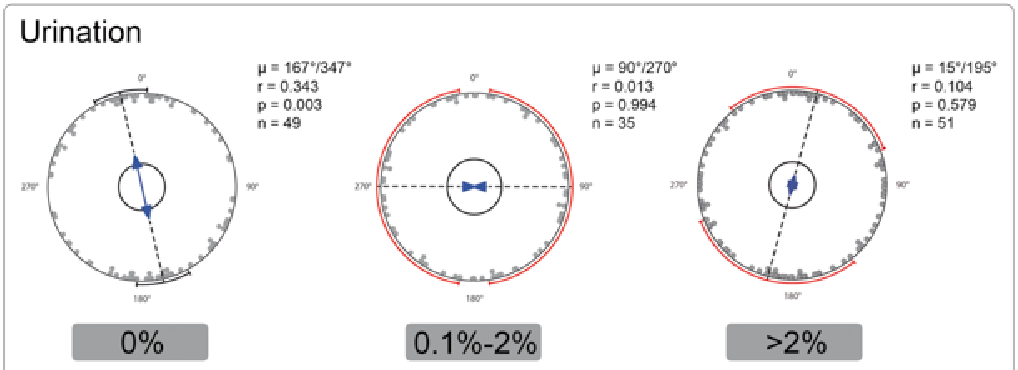

Figure 3 Analysis of dog body alignment during urination. Axial analysis of mean vectors of dogs of both sexes with at least five observations. Observations from three different categories of relative changes of the declination of the Earth's magnetic field are shown from left to right (0%, 0.1-2%, >2%). Each pair of opposite dots indicates the axis of the mean vector of all observations of a single dog. The direction (μ) and length (r) of the (grand) mean vector and the p-value of the Rayleigh uniformity test as well as the sample size are given next to each diagram. μ and r are indicated by the direction and length of the blue arrows, respectively. Small inner circles indicate the 5%-significance level of the Rayleigh test. Circle segments at the outer circle represent the 95%-confidence intervals (red circle segments indicate intervals that could not be calculated with confidence due to large circular standard deviations). A significant N-S axial orientation (i.e., 95%-confidence interval includes the N-S axis) can only be seen under conditions of zero declination change. See Tables for further details on statistics.

Table 8 Proportion of observations made under different conditions of the Earth's magnetic field expressed in rate of changes of declination during the sampling period

Declination changes (%)	Proportion of observations (%)
0	18
0.1-1.0	6
1.1-2.0	19
2.1-3.0	17
3.1-4.0	16
4.1-5.0	12
5.1-6	3
6.1-8.0	6
>8.1	3

observation was made when the sun was visible. Hence, with high probability (67%) most walks during the daylight period were made when it was cloudy.

Last but not least, the argument that the dogs might orient with regard to sun position so that they turn with their back to the sun in order to avoid dazzling by sunshine during such a sensitive and vulnerable act as excretion can be questioned. This argument is not plausible for urine marking, which is a brief act. We doubt that a dog that cares of not being attacked would always make sure to be turned away from the sun. The dog will likely look in that direction from where danger can most probably be expected - and this is for sure not always the direction away from the sun. In contrast to a human, the dog is relying also on its nose and its ears (in some breeds even more than on its eyes) when monitoring its surroundings - so we may expect that the dog heads with its nose and pinnae against the wind or in the direction of interest. Directing the pinnae and the nose may take priority over eyes. One can also often observe that dogs (especially during defecation) align in a certain direction, which is actually a different one from the direction of interest and they turn their head then in that other direction. Also we have to take into account that dogs are smaller than humans, they look at a different angle over the horizon and even in situations when we are dazzled, they might be not. Quite important: note also that the preference is axial - there are many cases when the dog actually looks southwards. There is no evidence for shift of the alignment axis during the day.

Table 9 Proportion of measurements of alignment sampled during 2 hrs-periods (and during the night) and proportion of measurements (from the total) sampled in respective periods under conditions of quiet magnetic field (i.e., with no changes in declination)

Period (time)	Proportion of all observations (%)	Proportion of observations under quiet MF (%)
05:01–07:00	2.2	1.6
07:01–09:00	9.9	12.2
09:01–11:00	26	18.5
11:01–13:00	16.8	6.3
13:01–15:00	11.5	12.8
15:01–17:00	13.6	20.8
17:01–19:00	10.3	5.8
19:01–21:00	7.9	18
21:01–23:00	1.3	2.8
23:01–05:00	0.5	1.2

It is still enigmatic why the dogs do align at all, whether they do it "consciously" (i.e., whether the magnetic field is sensorial perceived (the dogs "see", "hear" or "smell" the compass direction or perceive it as a haptic stimulus) or whether its reception is controlled on the vegetative level (they "feel better/more comfortable or worse/less comfortable" in a certain direction). Our analysis of the raw data (not shown here) indicates that dogs not only *prefer* N-S direction, but at the same time they also *avoid* E-W direction. The fact that larger and faster changes in magnetic conditions result in random distribution of body directions, i.e., a lowering of the preferences and ceasing of the avoidances, can be explained either through disturbing or conscious "shutdown" of the magnetoreception mechanism. From the two putative mechanisms that are discussed in birds and other vertebrates (radical-pairs and single-domain or superparamagnetic particles [30,31]) both might account for the observed alignment of the dogs and their sensitivity to declination changes.

An answer may lie in the biological meaning of the behavior: if dogs would use a visual (radical-pair based) magnetic map to aid general orientation in space as has been proposed for rodents [32], they might have the need to center/calibrate the map now and then with regard to landmarks or a magnetic reference. Aligning the map and the view towards North (or South) facilitates reading the map. Furthermore, calibration only makes sense when the reference is stable and reliable. We might think of this the same way as a human is stopping during a hike to read a map. When the map is blurred or the reference (perceived magnetic direction) is dispersed or moving due to magnetic disturbances, however, calibration is impossible. In the case of the dogs it thus would totally make sense to not pay attention to magnetic body alignment any more under conditions of a shifting magnetic field.

Conclusions

We demonstrate, for the first time (a) magnetic sensitivity in dogs, (b) a measurable, predictable behavioral reaction

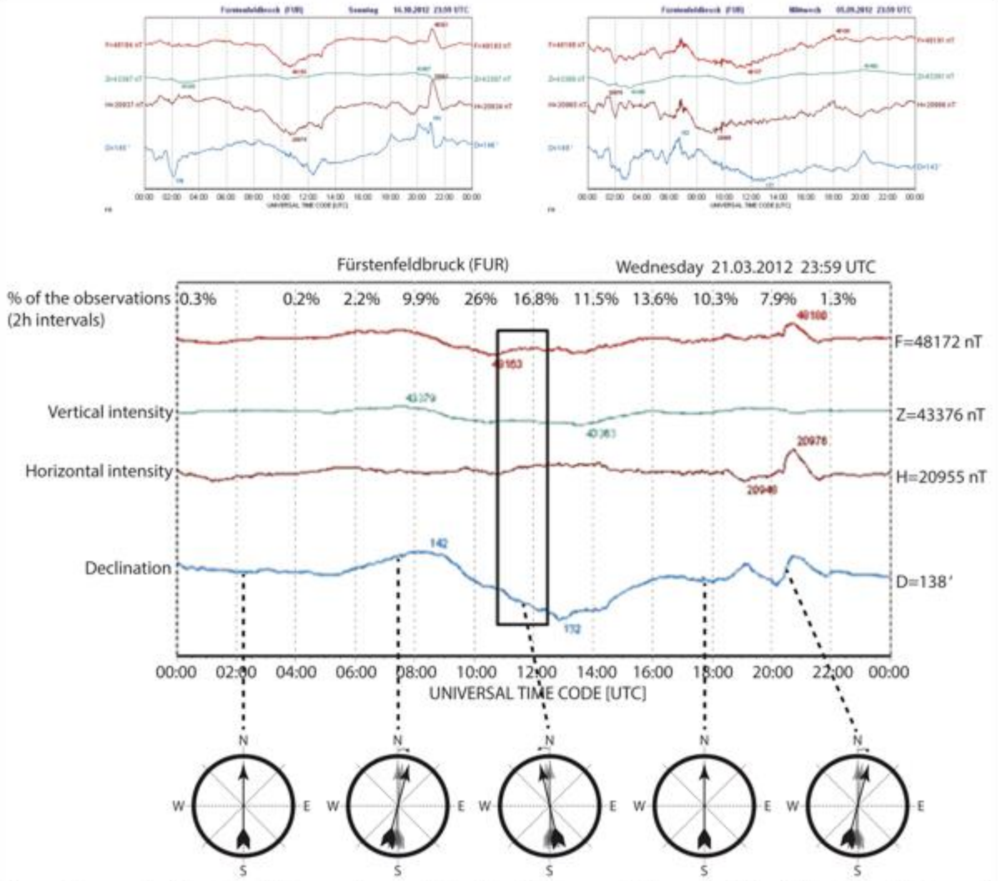

Figure 4 An example of three typical daily magnetograms obtained from the Geomagnetic Observatory Fürstenfeldbruck (Munich, Germany): http://www.geophysik.uni-muenchen.de/observatory/geomagnetism F = total intensity, Z = vertical intensity, H = horizontal intensity, D = declination of the Earth's magnetic field. In the given time period (marked by a rectangle in the lower graph), declination was changing westwards with the following rate: from 142 to 132 arch minutes in 240 time minutes = Difference of 10 arch minutes/240 min. = 4.2 %. The row of compasses illustrates the effect of the declination change in a highly exaggerated manner at different times of the day shown in the example. In reality, the changes in MF direction were much smaller. Note that even though the daily declination changes show some regularity (cf. ref. 22) they are not reliably predictable as illustrated by the frequent highly erratic changes, which are exemplarily shown in the two upper graphs.

upon natural magnetic field (MF) fluctuation in a mammal, and (c) high sensitivity to small changes in polarity, rather than in intensity, of the MF. Our findings open new horizons in magnetoreception research. The newly introduced animal model (dog), paradigm (alignment during excretion) and parameter (relative declination change) open new horizons for biomagnetic research. Particularly the findings that already small fluctuations in Earth's magnetic field elicit a behavioral response and the fact that "normal" magnetic conditions under which dogs express their orientation behavior occur only in about 30% of all cases call for caution. When extrapolated upon other animals and other experiments and observations on animal magnetoreception, this might explain the non-replicability of many findings and high scatter in others. Behavioral scientists need to revise their former experiments and observations and consider the phenomenon in their current and future experiments. The phenomenon challenges biophysicists to formulate testable hypotheses for mechanisms responsible for magnetoreception of inconsistencies

Table 10 List of recorded female dogs and respective numbers of records

	ID dog	Breed	Reporter (Abbrev.)	Age (years)	Weight (kg)	n defecation	n urination
1.	F22	Airedale Terrier	Hanz	4	25	39	14
2.	F06	Beagle	Nova	3	10	0	7
3.	F29	Beagle	Krej	7	10	92	52
4.	F01	Bearded Collie	Niets	11	25	102	30
5.	F23	Border Terrier	Hanz	13	7	15	2
6.	F69	Bouvier des Flandres	Elli	1	34	4	6
7.	F35	Dachshund	Hart	2.5	7	22	110
8.	F37	Dachshund	Faif	4	9	33	36
9.	F48	Dachshund	Bene	11	7	31	21
10.	F54	Dachshund	Bene	6	4	16	8
11.	F55	Dachshund	Bene	3.5	10	0	21
12.	F57	Dachshund	Bene	1	4	18	9
13.	F58	Dachshund	Bene	10	4	17	91
14.	F60	Dachshund	Bene	1	4	11	7
15.	F82	Dachshund	Bene	5.5	6.5	0	0
16.	F83	Dachshund	Bene	13	6	0	0
17.	F90	Dachshund	Dohm	2	4.5	5	42
18.	F40	Dalmatian	Kriv	14	20	64	153
19.	F21	English Springer Spaniel	Hanz	1	20	58	18
20.	F81	English Springer Spaniel	Zdar	7	21	0	0
21.	F77	Entlebucher Mountain Dog	Hron	4	18	0	34
22.	F41	Fox Terrier Smooth	Adam	12	8	37	75
23.	F42	Fox Terrier Smooth	Adam	2	6.5	33	39
24.	F43	Fox Terrier Smooth	Adam	6	8.5	20	65
25.	F44	Fox Terrier Smooth	Adam	2	10	16	16
26.	F36	German Spaniel	Faif	3	13	46	33
27.	F13	German Wirehaired Pointer	Cuko	4	30	5	0
28.	F14	German Wirehaired Pointer	Cuko	7	30	3	0
29.	F20	Golden Retriever	Hanz	10	30	29	16
30.	F39	Irish Terrier	Tres	1.5	15	15	16
31.	F24	Jack Russell Terrier	Jura	3	7	0	32
32.	F75	Mix	Hron	12	20	4	79
33.	F66	Mix: Lhasa Apso/Jack Russell Terrier	Rick	4	x	22	0
34.	F09	Rhodesian Ridgeback	Nova	5	30	0	59
35.	F71	Small Münsterländer	Pali	10	24	24	50
36.	F32	Standard Schnauzer	Posp	12	6	34	125
37.	F45	Tibetan Spaniel	Hegl	6	5	14	101
38.	F70	Transylvanian Hound	Zema	0.7	30	0	10
39.	F08	Weimaraner	Nova	6	30	2	71
40.	F10	West Highland White Terrier	Nova	3	7	0	42
41.	F34	West Highland White Terrier	Hart	8	7	56	212
42.	F11	Yorkshire Terrier	Garc	6.5	2	30	0
		records/dogs				*917*	*1702*

of the direction of the MF direction. Finally, it forces biologists and physicians to seriously reconsider effects magnetic storms might pose on organisms.

Methods

Alignment of the body (along the thoracic spine) in direction towards the head (heading) was measured in freely moving dogs (i.e., not on the leash) in "open field" (on meadows, fields, in the wood etc., i.e., unconstrained, and uninfluenced by linear structures, such as walls and fences) away from the road traffic, high voltage power lines, and conspicuous steel constructions during defecation and urination by a hand-held compass (Figure 4). Dog breed, sex, age, body mass, condition, dog-ID were protocolled as well as date, time, locality, and further circumstances of recordings (e.g. within the home range, in unfamiliar surroundings etc.). Thanks to the commitment of altogether 37 dog owners/reporters and the involvement of 70 dogs (28 males, 42 females) belonging to 37 breeds (Tables 10 and 11) we collected data on heading during defecation (n = 1,893 observations; 55 dogs) and urination (n = 5,582; 59 dogs) from December 2011 till July 2013. The samples were collected in the Czech Republic and in Germany.

After sampling and the first analysis (which yielded negative or at least ambiguous results) had been completed, we decided to sort the data according to the geomagnetic conditions predominating during the respective sampling times. Correlative values on Earth's magnetic field strength and direction for all the particular times of recordings were obtained from the Geomagnetic Observatory Fürstenfeldbruck (Munich, Germany): http://www.geophysik.uni-muenchen.de/observatory/geomagnetism

Data on K and C values expressing the magnitude of disturbances in horizontal intensity of the Earth's magnetic

Table 11 List of recorded male dogs and respective numbers of records

	ID dog	Breed	Reporter (Abbrev.)	Age (years)	weight (kg)	n defecation	n urination
1.	M27	Beagle	Krej	4	10	95	53
2.	M28	Beagle	Krej	2	10	92	53
3.	M33	Beagle	Posp	3	10	14	39
4.	M04	Bernese Mountain Dog	Leu	5	40	29	0
5.	M76	Border Terrier	Hron	7	8	0	37
6.	M07	Borzoi	Nova	4	40	96	2478
7.	M31	Coton de Tulear	Acke	4	4	11	106
8.	M05	Dachsbracke	Cerv	7	15	54	127
9.	M26	Dachshund	Komi	5	7	46	92
10.	M52	Dachshund	Bene	7	5	0	23
11.	M53	Dachshund	Bene	8	4	10	43
12.	M59	Dachshund	Bene	1	4	20	19
13.	M61	Dachshund	Bene	12	6	2	50
14.	M62	Dachshund	Bene	1	6	15	16
15.	M65	Dachshund	Faif	3	7	10	7
16.	M74	German Spitz	Hron	3.5	5	0	36
17.	M72	Hanoverian Hound	Krau	5.5	45	15	0
18.	M03	Irish Red Setter	Gros	3	30	47	0
19.	M80	Mix: German Shepherd x Schnauzer	Spor	10	35	71	85
20.	M63	Mix: Husky-Australian Shepherd	Rick	5	25	46	0
21.	M16	Norfolk Terrier	Kust	3	9	48	245
22.	M73	Norwich Terrier	Hron	3	8	0	36
23.	M46	Old English Sheepdog	Baum	4	45	38	122
24.	M19	Pug	Plac	3	9	66	60
25.	M25	Rhodesian Ridgeback	Jura	3	30	0	34
26.	M02	Schapendoes	Kour	1.5	25	86	84
27.	M30	Styrian Coarse-haired Hound	Kubi	7	15	45	19
28.	M38	Transylvanian Hound	Klem	0.5	30	20	16
		records/dogs				*976*	*3880*

Figure 5 Body orientation in dogs during defecation or urination was measured as a compass direction of the thoracic spine (between scapulae) towards the head. (We included the photo just to illustrate the measurement. Owing to the photographer's effort to shoot the photo with the sun from behind and to demonstrate the way of measurement, the dog on the photo looks away from the sun.) Photo Credits go to Jenny Ricken.

field were obtained from: ftp://ftp.ngdc.noaa.gov/stp/geomagnetic_data/indices/kp_ap/.

Relative declination and intensity changes during the respective dog walks were assorted into the categories according to the relative changes (in percent) calculated from graphs by dividing the difference between the initial and end (minimum/maximum) values by the duration (in minutes) of the respective period of changes (Figure 5).

Circular statistics were carried out with Oriana 4.02 (Kovach Computing). Both pooled individual data and means of particular dogs or walks were considered and analyzed. We performed angular and axial analysis on the measurements of each dog. Second order analysis was performed on the data which yielded the higher significance in the first order analysis (angular or axial). Only dogs with at least five measurements were analyzed. Statistically significant deviations from random distributions were investigated using the Rayleigh test of circular statistics. Differences between distributions were tested for significance with the Mardia-Watson-Wheeler test. Level of significance was set at 5%. Since about 44% data on urination under control conditions originated from one dog (M07, male borzoi) we also performed analyses for this particular dog separately.

Ethics statement

The study did not involve any disturbance of the animals under observation.

Competing interests

The authors declare that they have no competing interests.

Authors' contributions

Bur, Har, Nov conceived the study with significant input from Beg and Mal; All authors sampled data and/or coordinated sampling by assistants; Beg, Bur, Har, Mal, Nov carried out statistical analyses; Beg, Bur, Mal wrote the paper with input from Har and Nov; Bur discovered dependency of alignment upon Earth's magnetic conditions; All authors discussed the findings; Beg, Bur, Har, Mal, Nov interpreted the observations. All authors read and approved the final manuscript.

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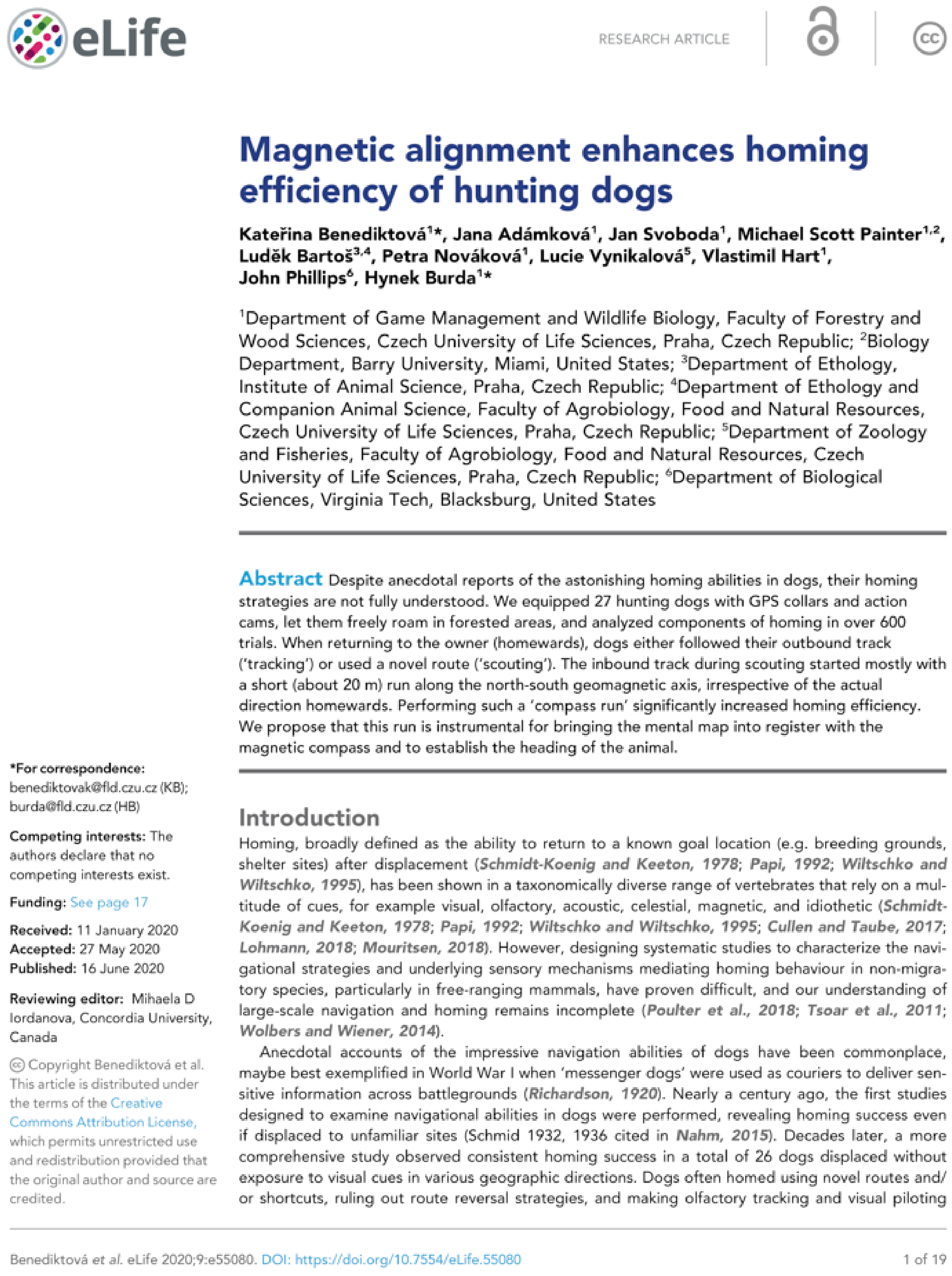
8.4 Příloha č. 4



eLife RESEARCH ARTICLE

Magnetic alignment enhances homing efficiency of hunting dogs

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Abstract Despite anecdotal reports of the astonishing homing abilities in dogs, their homing strategies are not fully understood. We equipped 27 hunting dogs with GPS collars and action cams, let them freely roam in forested areas, and analyzed components of homing in over 600 trials. When returning to the owner (homewards), dogs either followed their outbound track ('tracking') or used a novel route ('scouting'). The inbound track during scouting started mostly with a short (about 20 m) run along the north-south geomagnetic axis, irrespective of the actual direction homewards. Performing such a 'compass run' significantly increased homing efficiency. We propose that this run is instrumental for bringing the mental map into register with the magnetic compass and to establish the heading of the animal.

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Introduction

Homing, broadly defined as the ability to return to a known goal location (e.g. breeding grounds, shelter sites) after displacement (*Schmidt-Koenig and Keeton, 1978*; *Papi, 1992*; *Wiltschko and Wiltschko, 1995*), has been shown in a taxonomically diverse range of vertebrates that rely on a multitude of cues, for example visual, olfactory, acoustic, celestial, magnetic, and idiothetic (*Schmidt-Koenig and Keeton, 1978*; *Papi, 1992*; *Wiltschko and Wiltschko, 1995*; *Cullen and Taube, 2017*; *Lohmann, 2018*; *Mouritsen, 2018*). However, designing systematic studies to characterize the navigational strategies and underlying sensory mechanisms mediating homing behaviour in non-migratory species, particularly in free-ranging mammals, have proven difficult, and our understanding of large-scale navigation and homing remains incomplete (*Poulter et al., 2018*; *Tsoar et al., 2011*; *Wolbers and Wiener, 2014*).

Anecdotal accounts of the impressive navigation abilities of dogs have been commonplace, maybe best exemplified in World War I when 'messenger dogs' were used as couriers to deliver sensitive information across battlegrounds (*Richardson, 1920*). Nearly a century ago, the first studies designed to examine navigational abilities in dogs were performed, revealing homing success even if displaced to unfamiliar sites (Schmid 1932, 1936 cited in *Nahm, 2015*). Decades later, a more comprehensive study observed consistent homing success in a total of 26 dogs displaced without exposure to visual cues in various geographic directions. Dogs often homed using novel routes and/or shortcuts, ruling out route reversal strategies, and making olfactory tracking and visual piloting unlikely. Indeed, as previous authors have suggested, shedding light on the mystery of mammalian homing may require unconventional research approaches that focus on 'unusual' senses (***Nahm, 2015***).

Hunting dogs, particularly the so-called scent hounds, have been selected over generations to detect and pursue tracks of game animals and, if not followed by the hunter, to return to the place where the pursuit started, often over distances of hundreds or thousands of meters. How dogs pinpoint the owner's location using novel routes of return in highly variable densely forested habitats remains perplexing.

We expect that either dogs can find their way to the owner following their own scent trail back (a strategy called 'tracking') or they can perform true navigation, the ability to home over large distances without relying on route-based landmarks or information acquired during the displacement, a strategy we termed 'scouting', searching for a new way. While tracking may be safe, it is lengthy. Scouting enables taking shortcuts and might be faster but requires navigation capability and, because of possible errors, is risky.

Using GPS data complemented by video recordings by action cams, we analyzed orientation of free-roaming scent hounds. We expected to find evidence for either tracking or scouting, to test the predictions about the route length and duration, and to see indications for the type of decision made at the turning point. Furthermore, we expected that should visual piloting (orientation towards landmarks) take place there would be an effect of the height of the dog as higher (taller) dogs should have better overview (farther horizon) than lower dogs.

Altogether, 27 hunting dogs from ten breeds were equipped with a GPS collar and in several cases also with an action camera capturing a portion of the dog's head, thus providing information about its movement, behaviour, and the landscape in front of and around the dog (***Figure 1***, ***Video 1***). In total, 622 trials (excursions) were performed at 62 locations during diurnal walks in forested hunting grounds in the Czech Republic from September 2014 to December 2017. Based on the records, we determined turning points, dividing the whole excursion into the outbound and inbound tracks, and we measured azimuths at particular points, length and speed of particular tracks (***Figure 2A***).

Results

Return strategy

In 399 cases (59.4 %), dogs homed by following their outbound track (tracking strategy), and in 223 cases (33.2 %), dogs homed using novel route (scouting strategy). In 50 cases (8.0 %), dogs combined both strategies during a single return (***Figure 2B–C***). In this study, we focus only on 'scouting'.

Speed and track length

Scouting dogs were faster than tracking ones (***Figure 3***). As expected, taller dogs ran faster than smaller ones, but the shoulder height did not affect length of the inbound track (***Figure 4***) and the average speed of the inbound trajectory was faster when a portion of the return followed forest paths (***Figure 5***). Inbound track length was significantly longer when forest paths were used (***Figure 5***). Shoulder height did not affect inbound track length (***Supplementary file 1B***- Table 2). As expected, there was a positive correlation between direct ('beeline') distance between the turning point and the owner and the average inbound track length (***Figure 4***, ***Supplementary file 1B***- Table 2).

Azimuths and the 'compass run'

The compass directions in which dogs started the excursions (***Figure 2A***, azimuth A) and at the turning point relative to the excursion start, and thus to the goal (***Figure 2A***, azimuth B) were random, irrespective whether dogs were later tracking or scouting (***Figure 6***, ***Supplementary file 1E***- Table 5). The direction in which the dogs started to return (***Figure 2A***, azimuth C) was random in tracking dogs, but significantly aligned along the ~north-south magnetic axis in scouting dogs (***Figure 7***, ***Supplementary file 1E***- Table 5). Specifically, dogs homing by scouting started their return with a short (average length 18.1 m, ***Supplementary file 1D***- Table 4), 'compass run' aligned along the ~north-south geomagnetic axis (***Supplementary file 1E-F***- Tables 5-6, ***Video 2***).

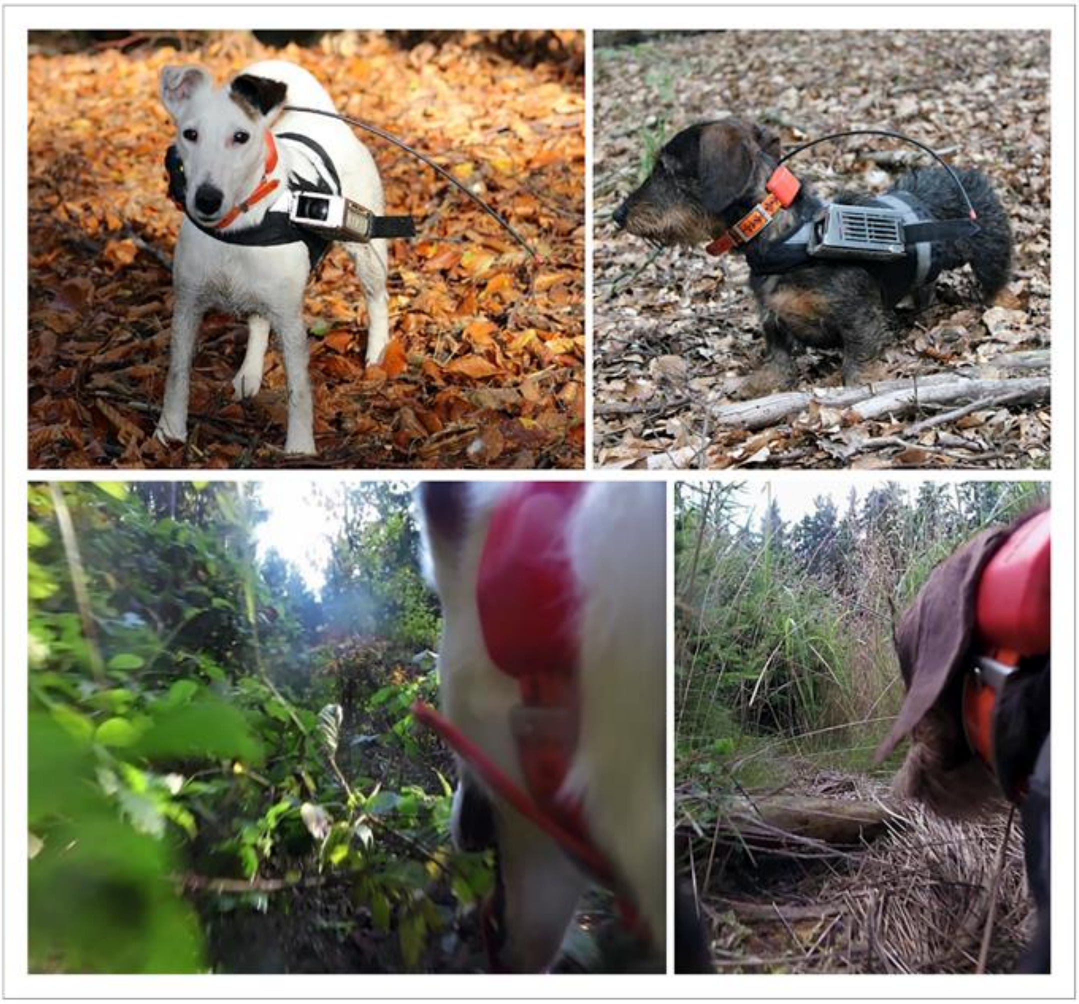

Figure 1. Still shots of a fox terrier (left column) and a miniature dachshund (right column) used in this study showing the tracking equipment and habitat. Above: The GPS transmitter and antenna are fixed to a collar and fitted around the animal's neck (note that for safety and comfort of the animal, the collar is free to rotate). The black fabric harness is secured around the torso and chest and is used to attach the protective camera case containing the camera and battery. Below: A typical field of view captured by the video camera that includes the dog's head/neck, and provides a detailed view of the surrounding terrain. An on-board microphone (not visible) is used to record audio.

To determine if the position of the owner influenced the orientation of the compass run, we partitioned the data into four distributions (north, south, east, or west, + / - 45˚), according to the location of the owner relative to the turning point. In all four distributions, the compass run was significantly orientated along the ~north south geomagnetic axis, suggesting that its orientation was independent of the direction to the owner (***Figure 8***, ***Supplementary file 1F***- Table 6).

Video 1. Example of all three phases of an excursion. Labels of the left side of the video indicate the segment of the excursion. The video begins with the excursion start (i.e. the beginning of the outbound trajectory) when the dog becomes separated by >100 m from the owner, at which point the owner remains stationary in the forest. Shortly after, the dog detects and follows the olfactory track of a wild game animal, indicated by barking behaviour. After the outbound trajectory, the dog begins the turning trajectory phase of the excursion (see Materials and methods) and the turning point is shown when the dog briefly pauses. This location marks the beginning of the compass run (=alignment run, azimuth C, initial inbound segment). Lastly, the inbound trajectory is shown representing the phase when the dog is homing back to the location of the excursion start/owner.
https://elifesciences.org/articles/55080#video1

There were no significant differences in axial preference of the compass run between sexes (Watson's U^2 test, U = 0.027, p>0.5) or between familiar and unfamiliar areas (Watson's U^2 test, U = 0.036, p>0.5).

The probability of exhibiting a scouting strategy after compass run was aligned along the north-south axis was almost four times higher than the probability of exhibiting tracking (odds ratio = 3.60, p<0.0001) (***Figure 7E***, ***Supplementary file 1B***- Table 2). No other factors appeared influential.

Importantly, when the compass run was aligned along the ~north-south axis, homing was more efficient, i.e., the ratio between the length of the inbound track and the shortest distance between the turning point and the goal was significantly reduced compared to the ~east-west compass runs (F = 6.47, p=0.01) (***Figure 9 Supplementary file 1B***- Table 2).

Effect of sex, breed and study site familiarity

We partitioned the data by sex for all individuals and used a Rayleigh test to determine if sex influence the orientation of the 'compass run' (***Figure 2***, azimuth C) during scouting returns. There was no significant difference between the two resulting distributions (Watson's U2 test, U = 0.027, p>0.5), and therefore, no sex differences in the orientation of the compass run.

Sex and breed did not influence the probability of return strategy used during homing (GLMM, p>0.05). Furthermore, we tested whether study site familiarity influenced the orientation of the compass run. We grouped azimuth C into two groups, according to whether the dog had visited the study at least one time prior to the excursion or if the dog was experiencing the study site for the first time. No differences between the two distributions (familiar vs unfamiliar) were found (Watson's U2 test, U = 0.036, p>0.5).

Effect of sun

To test for an effect of sun and/or polarized light on the orientation of the compass run during scouting returns, the sun position was determined by estimating the sun's azimuth during the 15th day of each month, therefore accounting for seasonal variation in azimuth position (sun position data was taken from a central location in the Czech Republic, central to the locations of all test sites). Next, the sun azimuth direction was recorded for each hour during the 15th day of each month, for all available daylight hours. Thus, we created an average sun azimuth direction for each month of the year, with one-hour resolution. For circular analyses, we pooled the orientation of azimuth C relative to the sun position for each excursion, using the nearest hour of sun position according to each excursion time. A Rayleigh test was used to determine if the distribution of azimuth C was non-random when plotted relative to sun position. The position of sun, and thus polarization pattern, did not significantly influence the orientation of azimuth C during scouting returns at the individual level (n = 251, μ = 69°/249°, r = 0.04, p=0.673) or at the group level (n = 27, μ = 146°/326°, r = 0.021, p=0.989).

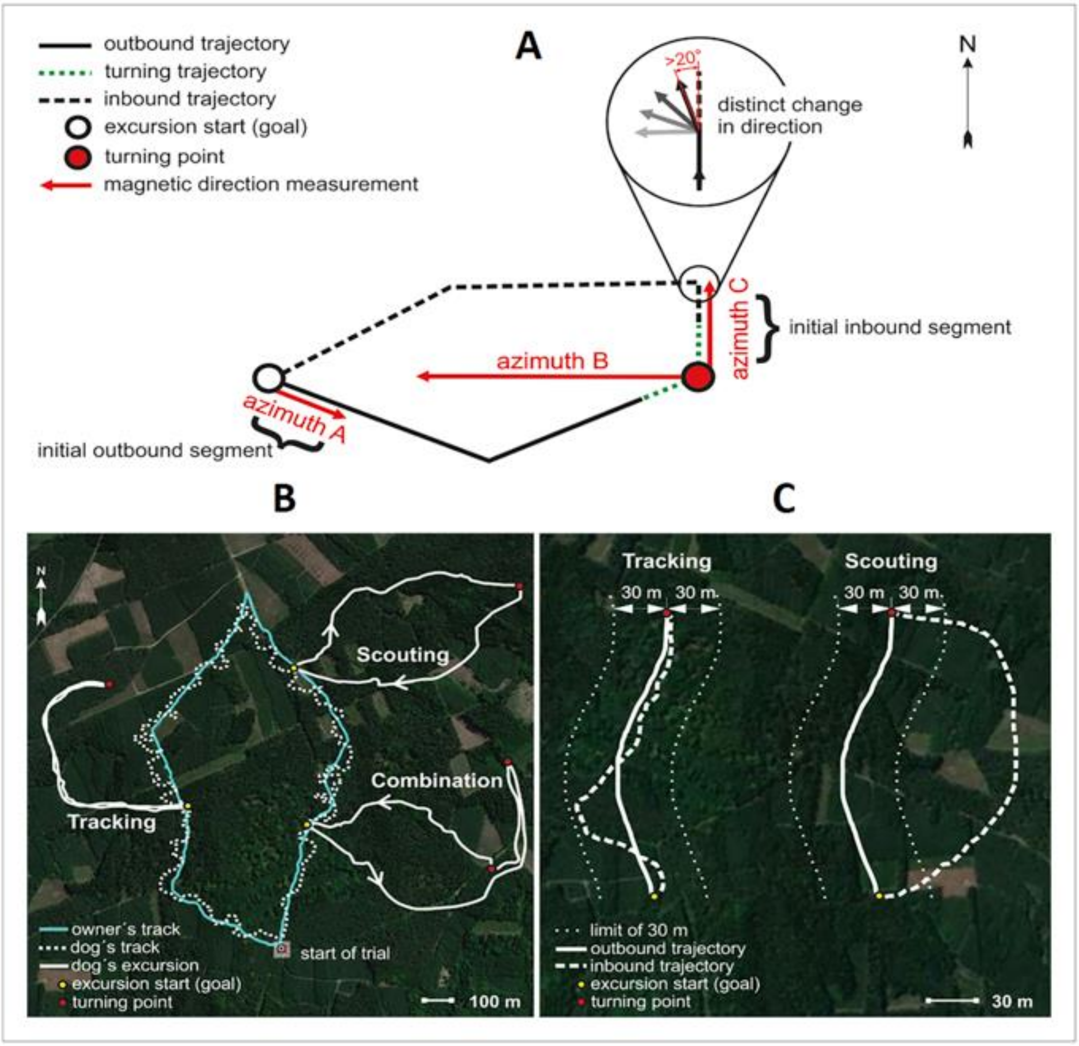

Figure 2. Spatial features and return strategies derived from GPS data used in analyses. (**A**) Schematic illustration of total excursion track. Excursion start marks location of owner when the dog is more than 100 m away, indicating that the dog is pursuing a game animal. Excursion start also marks the approximate location where the owner remains hidden until the dog returns. Turning point represents the location where the dog initiated its return to the owner. Azimuth A represents the magnetic direction of the initial outbound segment, calculated between the excursion start and the GPS point recorded 5 s after the excursion start. Azimuth B represents the magnetic direction of the owner relative to the dog at the turning point. Azimuth C represents the magnetic direction of the initial inbound segment, the 'compass run', calculated by measuring the direction between the turning point and the point where the dog exhibits a distinct (>20˚) deflection in track direction (magnified inset). See Materials and methods for additional details. (**B**) GPS tracks showing examples of Tracking and Scouting strategies or combination of strategies. Solid white tracks show excursions. The turquoise line shows the owner's track and the white dotted line shows the dog's track during non-excursion portions of the trial. (**C**) Examples of Tracking and Scouting return strategies: Tracking: inbound return track falls within a ± 30 m corridor limit (shown by small white dots flanking each side of the track) of the outbound track. Scouting: the inbound return track is separated from the outbound trajectory by at least 30 m.

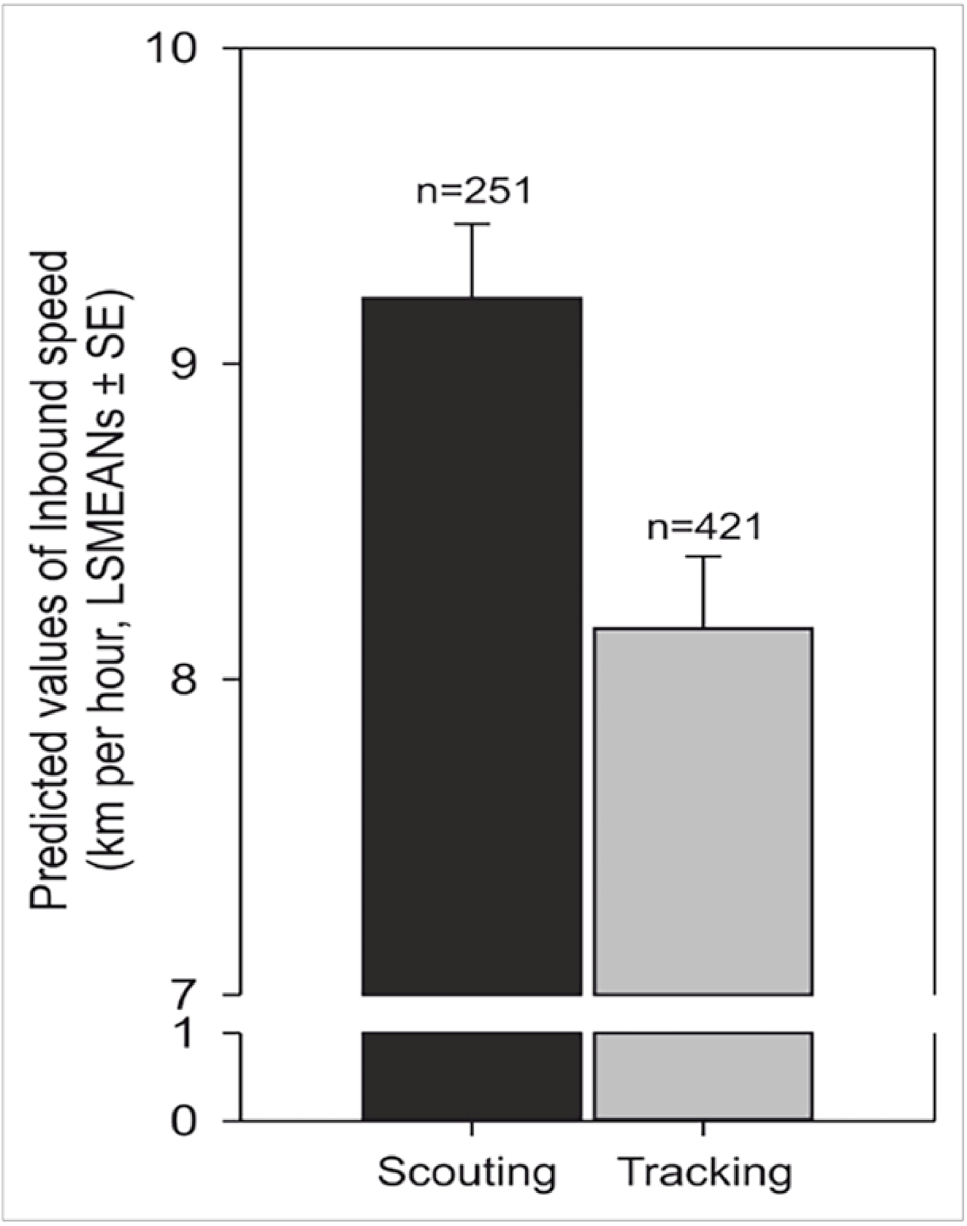

Figure 3. Average speed increases in scouting compared to tracking. Predicted values of inbound speed (km/hour, LSMEANs ± SE) according to return strategy and independent of the direction of the compass run (azimuth C).

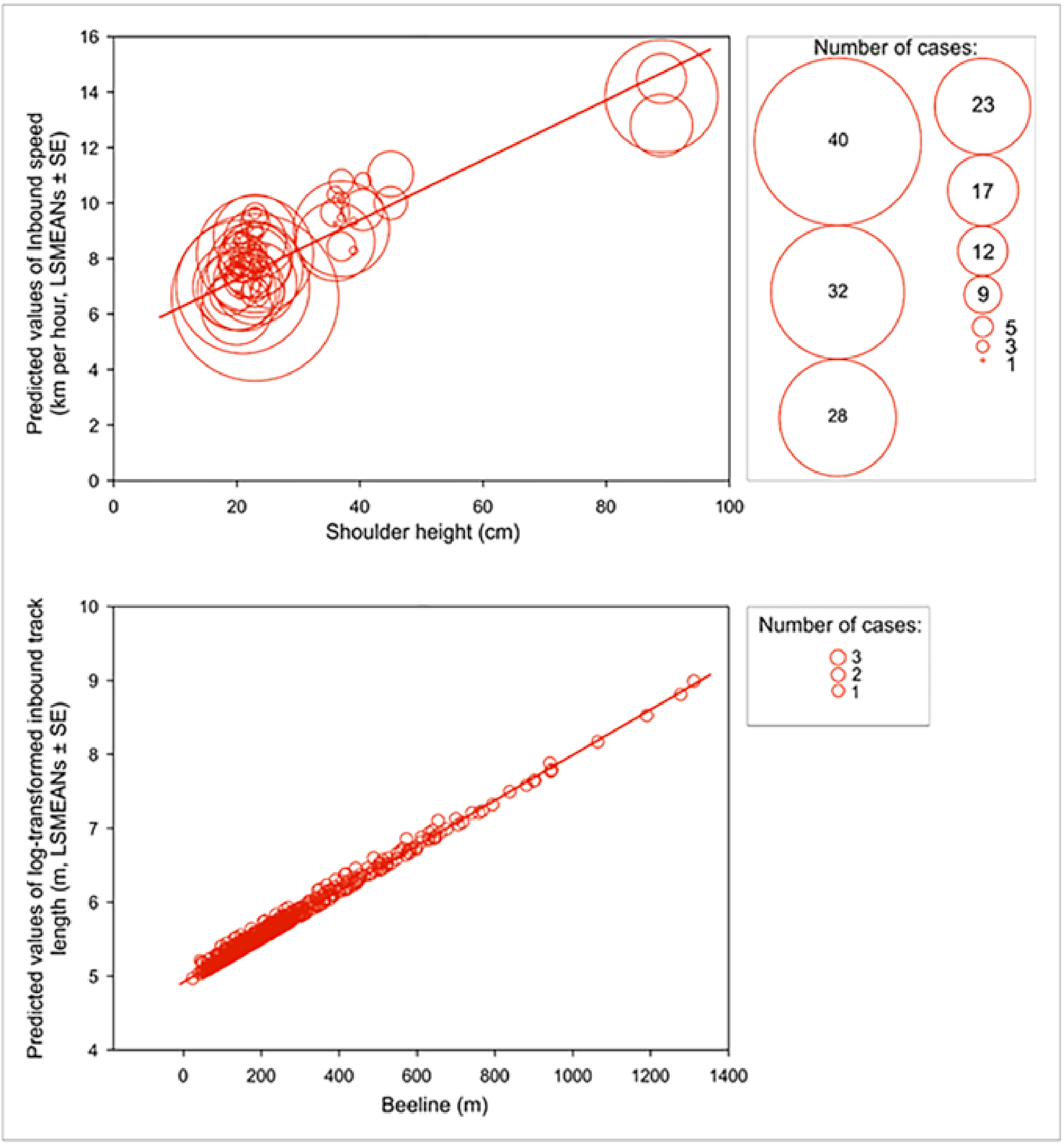

Figure 4. Inbound speed and track length positively correlate with shoulder height and beeline excursion distance, respectively. Upper row: A bubble-plot of predicted values of inbound speed (km per hour, LSMEANs ± SE) plotted relative to shoulder height (cm). The center of each bubble represents the predictive value and bubble size represents the number of cases for that value. Size class scale is shown on the right. Bottom row: A bubble-plot of predicted values of log-transformed total inbound track length (m, LSMEANs ± SE) as a function of direct ('beeline') distance between the turning point and the owner. The center of each bubble indicates the predictive value and bubble size is equivalent to the number of cases, as shown in the box on the right.

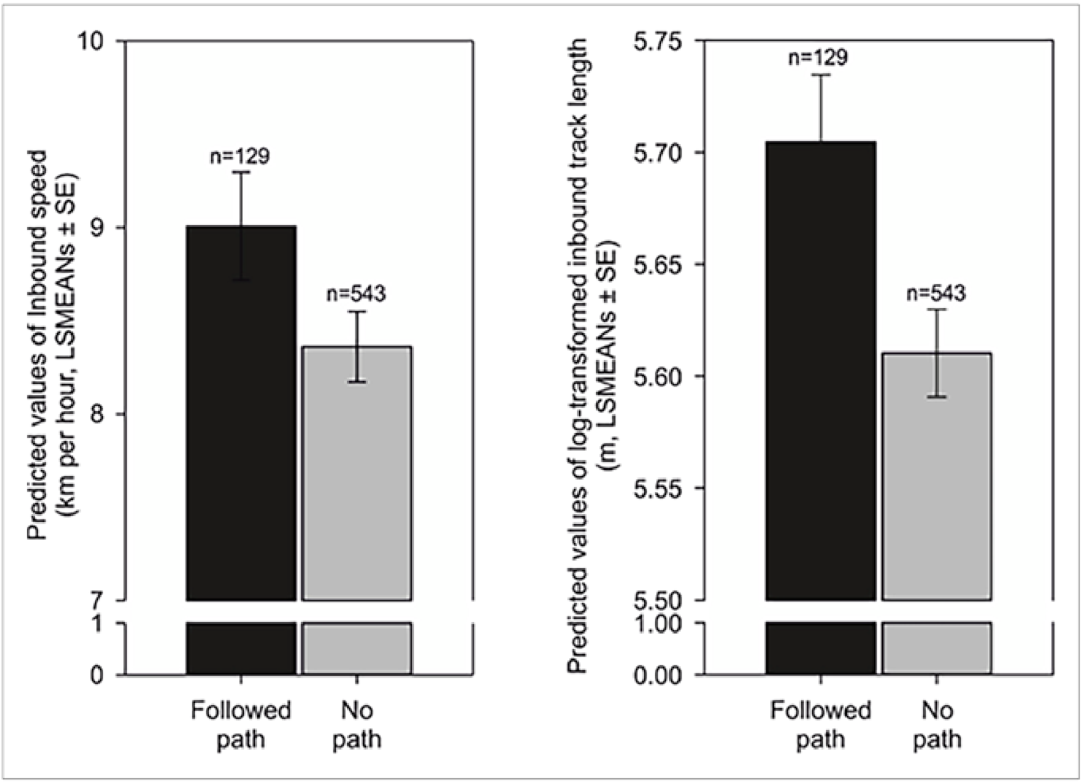

Figure 5. Inbound speed (length) and inbound track length (right) influenced by forest paths during the homing return. Left: Predicted values of inbound speed (km per hour, LSMEANs ± SE) grouped according to whether a portion of the inbound trajectory followed a forest path ('Followed path'), or if the return was completed without the use of a forest path ('No path'). Right: Predicted values of log-transformed total inbound track length (m, LSMEANs ± SE) between returns when at least a portion of the inbound track followed a forest path compared to returns when no forest paths were used.

Effect of wind

Wind direction was recorded at the study site for each excursion by the owner. To test for an effect of wind direction, particularly in conditions when wind was blowing from the owner to the direction of the dog at the turning point, we used a Rayleigh test to determine if the wind direction was non-random across excursions when dogs used a scouting return strategy. In 55 cases (22 % of all scouting excursions), no wind was detected and therefore these excursions could not be included in the analyses. For the remainder of excursions (n = 196), Azimuth B (i.e. direction between the turning point and owner) (***Figure 2***) was plotted relative to the wind direction.

Partitioning the circular data into eight equal bin sizes (each bin ±22.5˚ and centered on the 45's, i.e. 0˚, 45˚, 90˚, 135˚, etc.), we found that the wind conditions in only 24 scouting returns (<10 % of scouting returns) were suitable for olfactory piloting to the owner (i.e. <10 % of scouting returns had wind conditions where the wind was blowing in the direction (±22.5˚) from the owner to the dog at the point of return/start of azimuth C.

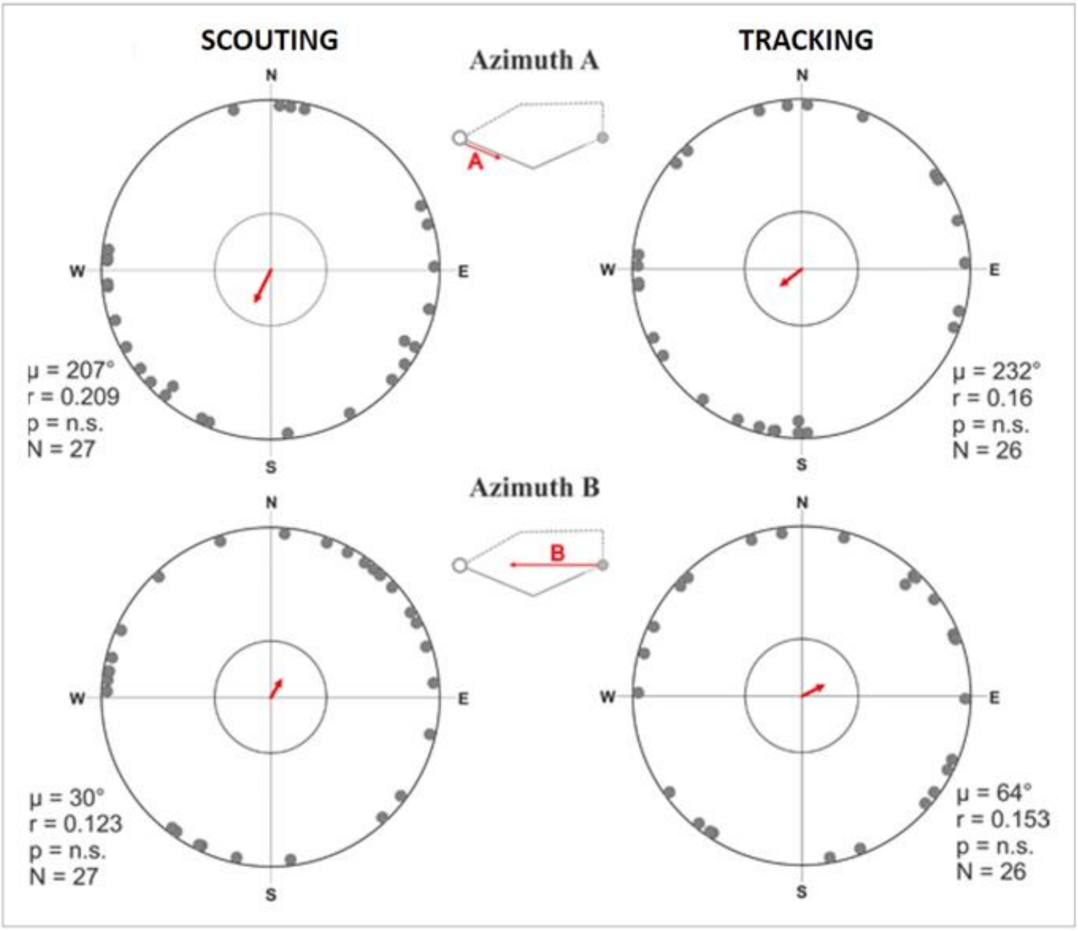

Figure 6. Circular distributions for azimuth A and azimuth B means grouped by return strategy. Circular distributions of magnetic orientation of the direction of the turning point relative to the excursion start/owner (azimuth B) and the initial outbound segment (azimuth A) for scouting (left column) and tracking (right column). The small schematics centered between each plot show the vector corresponding to the data in each distribution. The red arrow indicates the angular vector (μ) calculated over all angular means. The length of the mean vector (r) corresponds to the degree of clustering in the distribution on a scale of 0.0–1.0, where the circular plot radius = 1.0. The inner circle marks the 0.05 level of significance limit computed using the Rayleigh test.

Discussion

We found that dogs returning in a forest either follow back their outbound trajectory, a strategy called *tracking* or chose a completely new route, a strategy called *scouting*. In this study, we analyzed only scouting events and found a conspicuous phenomenon. In most cases, dogs start their return with a short (about 20 m long) run, called here *compass run*, mostly performed along the north-south axis irrespective of the actual homeward direction.

It is unlikely that the direct involvement of visual, olfactory or celestial cues can explain the highly stereotyped and consistent ~north south alignment of the compass run. For example, the forested habitat and dense vegetation of the study sites make visual piloting unreliable and, in many cases,

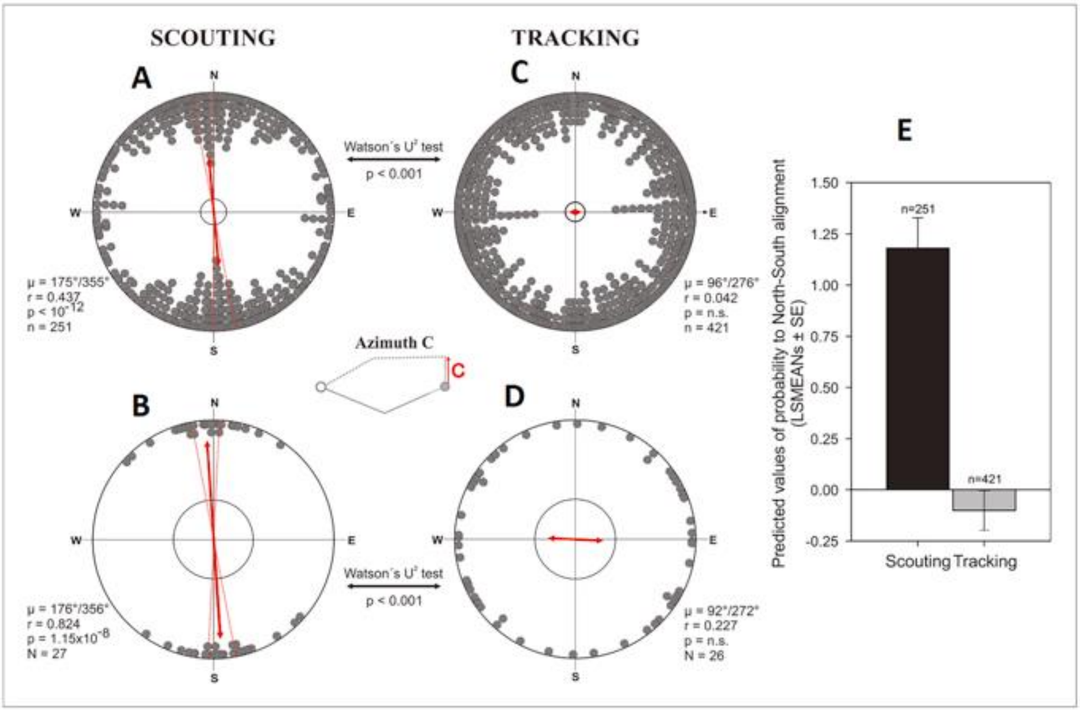

Figure 7. Alignment responses during the initial inbound return (= 'compass run') in free-roaming dogs. (**A–D**) Circular distributions showing geomagnetic alignment responses during the initial inbound segment (azimuth C, 'compass run'), when distributions are partitioned into Scouting (**A, B**) and Tracking (**C, D**) return strategies. Grey bearings plotted on the periphery of the distributions represent the axial orientation of compass runs for each excursion (**A, C**), each bearing treated as an independent data point, or (**B, D**) the axial orientation of compass runs when the mean orientation was first calculated for each dog. All data are plotted relative to magnetic north, indicated at the top of each plot, and the red double-headed arrow indicates the mean axial vector (μ) for each distribution. The length of the mean vector (r) corresponds to the degree of clustering around the mean and ranges from 0.0 to 1.0, with the radius of each plot = 1.0. Dashed red lines represent the 95% confidence intervals and the inner grey circle marks the p=0.05 level of significance limit computed using the Rayleigh test. Results from Watson's U^2 tests are shown between distributions, revealing significant differences in the compass run orientation between tracking a scouting return strategies. The small schematic centered between the plots shows azimuth C and the axial direction of the red vector corresponds to the orientation data plotted in each distribution. (**E**) Predicted values of the probability that dogs will exhibit a compass run along the ~north south geomagnetic axis (±45˚) during the initial inbound segment (LSMEANs ± SE) according to return strategy.

not possible. Furthermore, there was no effect of the body height (and thus the degree to which the dog's field of view of its surroundings was limited) on the probability of north-south alignment when compared to east-west alignment, a fact which is not consistent with a visual piloting hypothesis. Highly variable wind conditions, coupled with turbulence in the forest understory, rule out the use of olfactory piloting during scouting. In many cases, the Sun's disk was fully obstructed by cloud cover and/or overhead vegetation, making it challenging to use a sun or polarized light compass. And, although polarized light has been shown to calibrate the magnetic compass in bats (**Greif et al., 2014**), detection of skylight polarization is not thought to be widespread in mammals (**Horváth and Varjú, 2004**; **Marshall and Cronin, 2011**). More generally, it is difficult to reconcile what advantage a north-south orientation response would provide for any of the sensory modaities discussed above.

In contrast, the Earth's magnetic field provides a stable, omnipresent cue, regardless of daily or seasonal temporal variation, visual cue availability or weather conditions. The north-south alignment of the compass run in dogs is consistent with a wealth of studies providing support for spontaneous

Video 2. Example video showing the compass run behaviour during a scouting strategy return. The GPS track is shown on the right half of the video with the red 'bulls-eye' tracker synced with the video shown on the left. The bulls-eye tracker moves across the track corresponding to the position of the dog in the video. The checkerboard square represents the location where the video ends, but does not represent any relevant features/landmarks used for analyses. Compass and GPS measurements are shown on the left and are synced to the video and bulls-eye tracker. Yellow labels appear superimposed on the right side of the screen to indicate relevant features of the excursion. Before reaching the turning point, the dog is travelling in a ~ west northwest direction. As shown, the compass run (=alignment run, azimuth C) starts at the turning point and the dog begins its initial inbound segment in the ~north direction. The compass run is terminated at 0:22 when the dog changes magnetic direction by >20˚ (see Materials and methods) and the inbound trajectory continues as the dog navigates back to the owner (not shown).
https://elifesciences.org/articles/55080#video2

magnetic alignment along the north-south magnetic axis in a range of vertebrates in the field (reviewed in ***Begall et al., 2013***; ***Malkemper et al., 2016***) as well as in the laboratory under controlled conditions (e.g. ***Burda et al., 1990***; ***Phillips et al., 2002***; ***Muheim et al., 2006***; ***Malkemper et al., 2015***; ***Painter et al., 2018***).

While the functional significance of magnetic alignment is not fully understood, magnetic alignment may help to organize and structure many aspects of spatial behaviour (***Begall et al., 2013***). This may help to explain the compass run at the beginning of homing in scouting dogs. Indeed, several recent studies have shown that dogs are sensitive to magnetic cues (***Hart et al., 2013***; ***Adámková et al., 2017***; ***Martini et al., 2018***), and behavioural studies show that Earth-strength magnetic fields play a direct role in homing responses also in the blind mole-rat, a subterranean mammal (***Kimchi et al., 2004***). Taken together, we propose that the compass run is mediated by magnetic cues, and it helps to increase the accuracy and reduce the complexity of long-distance navigation across unfamiliar and/or highly variable environments.

Noteworthy, scouting dogs in unfamiliar locations cannot use visual landmarks to recalibrate a path integration system. Therefore, in the absence of familiar landmarks, the compass run may serve to recalibrate a path integration system relative to Earth's magnetic field, so that errors accumulated during the outbound trajectory are not incorporated into the estimate of the homing direction. Importantly, dogs in our study were not passively displaced as is usual in most homing experiments (***Tsoar et al., 2011***; ***Ostfeld and Manson, 1996***), and therefore, the involvement of path integration seems plausible, and may be one of several reasons why the compass run has not been identified in previous studies.

Our findings clearly show the importance of further research on the role and involvement of magnetic cues in canine (and more generally mammalian) navigation. More specifically, the research suggests that the magnetic field may provide dogs (and mammals generally) with a 'universal' reference frame, which is essential for long-distance navigation and arguably the most important component that is 'missing' from our current understanding of mammalian spatial behaviour and cognition.

Materials and methods

Study subjects

A total of 27 hunting dogs (10 M, 17 F) from ten breeds were used in the study (***Supplementary file 1A***- Table 1). All dogs come from breeds with pedigrees in hunting and animal tracking and were regularly assessed by veterinarians throughout the study. These dogs innately detect and pursue the olfactory tracks of game, and in rare cases, dogs were able to spot game animals from a distance (i.e. >20 m) through the forest. However, the small breeds used in this study are unable to keep pace with the much larger and faster game animals. Therefore, dogs were almost immediately left to rely on olfactory tracking and never posed any physical threat to wild animals.

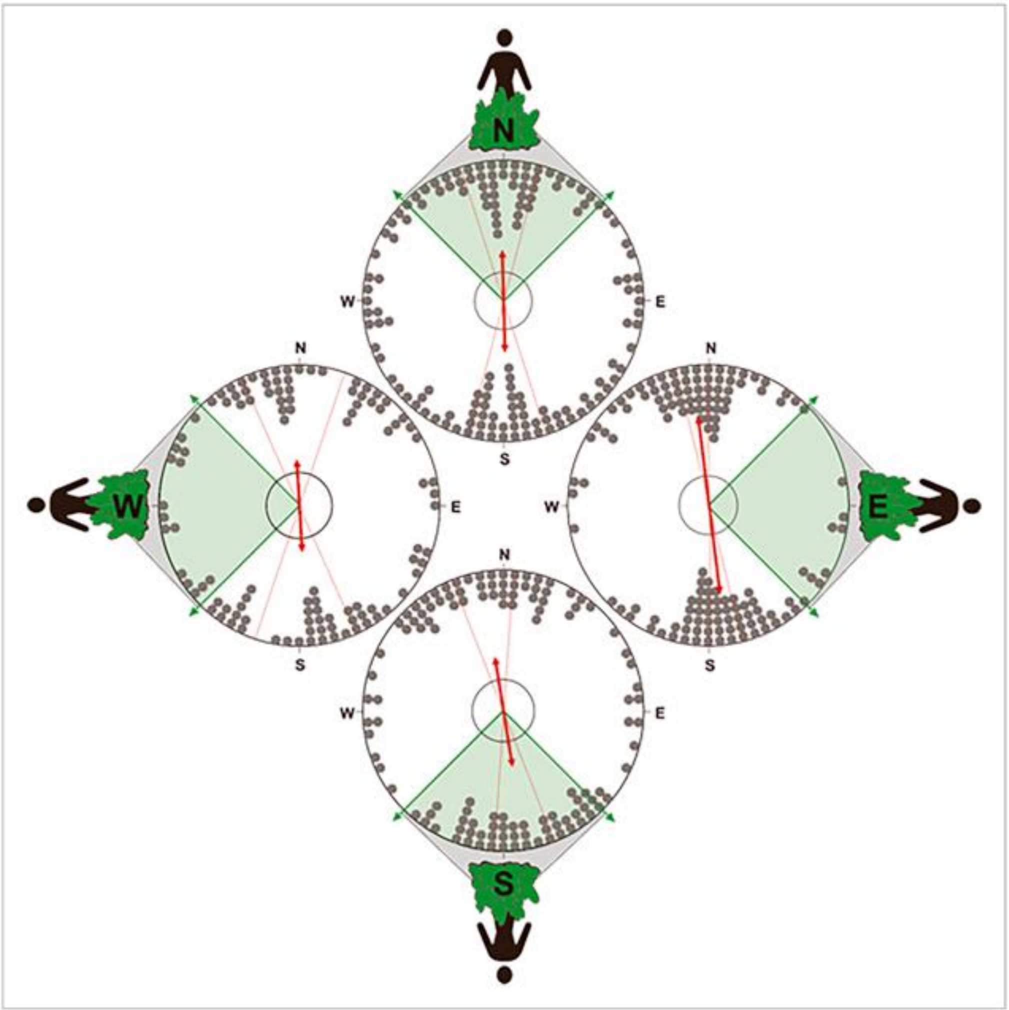

Figure 8. Orientation of the compass run plotted relative to the position of owner. To test for an influence of the owner on the orientation of the compass run (azimuth C) during scouting, the data was partitioned into four distributions corresponding to when the owner was located at one of the four cardinal compass directions (±45°) relative to the turning point. Therefore, the distributions above show the orientation of azimuth C when the owner is positioned at magnetic ~north (316°–45°),~east (46°–135°),~south (136°–225°), or ~west (226°–315°) relative to the turning point (i.e. relative to the start of the compass run). If the N-S orientation of the compass run is a direct response to the owner (i.e. olfactory or visual piloting towards the owner), then in situations when the owner is located along the ~east west axis relative to the turning point, the orientation of the compass run should also align along the ~east-west axis. Alternatively, if the compass run is independent of the owner, then there should be no statistical difference in the orientation of azimuth C when the owner is position in different magnetic directions. Each distribution plots the axial bearings recorded from each excursion. The position of the owner relative to azimuth C is shown on the outside of each distribution and the shaded section of each plot bounded with green arrows shows the range of possible positions of the owner in each distribution (45° range centered on each cardinal compass direction). All other symbols are identical to those in ***Figure 6***. Note that the axial bearings have been rounded to the nearest 5° only to facilitate the graphical representation of the responses and all statistics were calculated using data values measured to 1° resolution.

Tracking equipment

Dogs were equipped with a Garmin T5 mini (or DC50) GPS collar (Garmin Ltd., USA) fitted around the neck and programed to record GPS positions at 2.5 or 5.0 s intervals (GPS accuracy ±4.2 m based on ground-truth measurements collected at study site locations). A portion of the trials (31 %) were carried out using a Garmin Virb Elite action camera (Garmin Ltd., USA) housed inside a non-magnetic stainless steel mount fixed to the side of a custom-fitted fabric harness (**Figure 1**). The camera captured a similar field of view to that of each dog (**Figure 1**), and thus provided information about the dog's visual surroundings, including habitat characteristics. In addition, a portion of the dog's head was also captured, providing information about the dog's behaviour and movement (e.g. activity, head scanning, head orientation) and an on-board microphone detected barking behaviour, an indicator that the dog was in pursuit of a game track (**Video 1**). The customized harness was designed to minimize discomfort and allowed full mobility for all dogs. Dog owners were equipped with a handheld Garmin Alpha 100 or Astro 320 receiver (Garmin Ltd., USA) used to monitor and record GPS tracks.

Experimental procedure

A total of 622 trials were performed in forested hunting grounds at 62 independent locations in the Czech Republic from September 2014 to December 2017. All trials were performed with a single dog (i.e. trials were not carried out with groups of dogs), in areas free from high voltage power lines, paved roads or buildings, and at different times of day (daylight hours only) and different times of year. Dogs were transported to each site by a car and were given a 10 min rest and acclimation period in the close surroundings of the car (<20 m radius). Dogs were then equipped with the GPS collar, and in some cases, the harness-camera setup, and walked off-leash alongside the owner into the surrounding forest. Dogs could freely roam and explore the area to search for wild game tracks using olfactory cues, as is an innate behaviour in this context for the breeds used in this study. The following game animals are common in the study region: fallow deer (*Dama dama*), red deer (*Cervus elaphus*), roe deer (*Capreolus capreolus*), wild boar (*Sus scrofa*), European hare (*Lepus europaeus*), and red fox (*Vulpes vulpes*). During the search period, owners did not provide visual or acoustic commands to instruct the dog. The handheld GPS device was programmed to indicate when the dog had travelled $\geq$100 m from the position of the owner. At this moment (designated as 'excursion start') the owners stopped walking and marked their location on the handheld GPS. Owners then hid behind trees or dense vegetation within a 10 m radius from the 'excursion start' to minimize the possibility of visual piloting by dogs in final stages of their inbound return (see below). The owners remained at this place until the dog returned. The location of each trial, the dog's familiarity with the location, and weather conditions (wind speed, wind direction, and temperature) were recorded. Locations visited for the first time were considered to be unfamiliar, whereas dogs who had visited the location at least once previously were considered familiar with the area. The entire trial, including excursions (see below), lasted between 30 and 90 min.

Analysis of excursions

Identifying excursion features

'Excursions' are defined as the track recorded between the excursion start (see above) and the point when the dog started its return to the owner, staying at, or within 10 m from the excursion start (**Figure 2**). All excursions were analyzed using Garmin BaseCamp 4.6.2 software (Garmin Ltd., USA). In very rare cases when dogs did not return to the owner, they were found via GPS position and excluded from further analysis (n = 16, 2.4 % of all excursions).

Based on preliminary analyses of GPS tracks used to standardize the study protocol, excursions were divided into three distinct phases: 1) *outbound trajectory*: from the excursion start to the point where the dog terminates its pursuit of the game track; 2) *turning trajectory*: the part where the dog initiates its return to the excursion start/owner; within this part, we narrowed the *turning point*; 3) *inbound trajectory*: the return track to the owner (**Figure 2A**). We expected that turning trajectory (and specifically turning point) would be characterized by slowing down, perhaps even short stop as the dog orientates.

The whole excursion length (=100 %) was divided into ten equidistant segments (i.e. each segment encompassing 10 % of the total excursion length). The average speed over each segment was

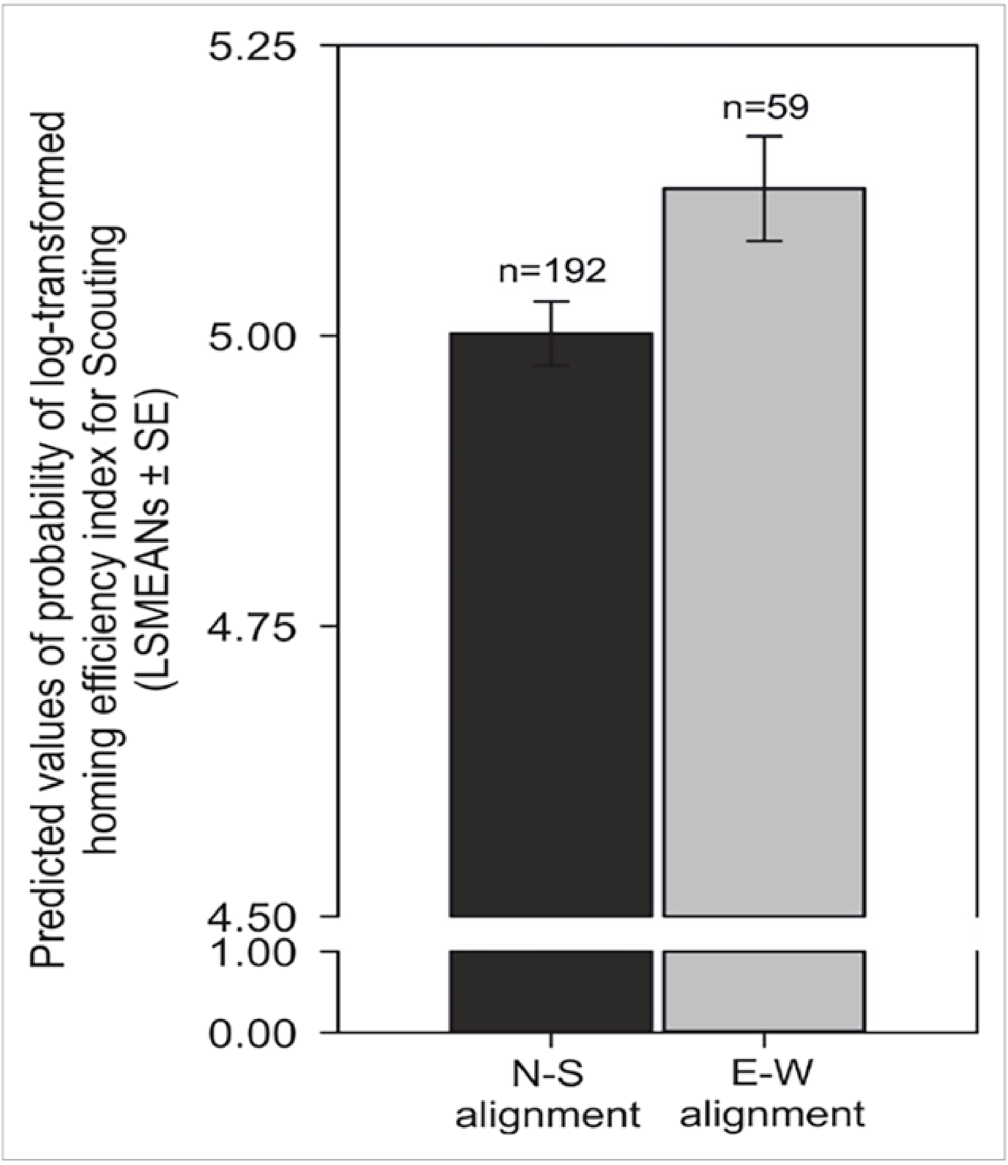

Figure 9. Compass run improves homing performance during scouting. Comparison of predicted values of the probability of log-transformed homing efficiency index (LSMEANs ± SE) between dogs exhibiting a compass run oriented along the ~north south (±45˚) compared to orientation along the east-west (±45˚) axis during scouting return strategies. The efficiency of homing is expressed as the ratio (%) between the length of the dog's inbound trajectory and the direct (beeline) distance between the turning point and the excursion start/owner. Titles and legends to supplementary videos.

calculated and the segment with the slowest speed was labelled as the *turning trajectory*. If the so determined place seems to be improbable (either too close to the start/goal or the dog pauses relatively long at one point) we checked the situation at video to exclude the possibility that the dog stopped to drink, bath, sniff at some interesting place or encountered difficult terrain. If this was the case or video was not available, the second slowest segment was identified as the turning trajectory (n = 26,<5 % of all excursions). If this segment was also located near the excursion start/owner, the respective situation was again checked at the video if available, and/or the slower segment with the farthest straight-line distance from the excursion start was labelled as the turning trajectory (n = 53, 8.5 % of all excursions).

Within the turning trajectory, the average speed was calculated between each successive GPS point. The point-to-point path within the turning trajectory with the slowest speed was identified and marked as the *turning point*, representing the specific location where the dog initiated its return to the owner (***Figure 2A***, ***Video 2***).

The focus of the current study was to evaluate long-distance navigation in free-roaming dogs, and therefore, excursions shorter than 200 m were excluded from the analyses.

Identifying azimuths

All magnetic measurements used in the analyses were made using measurement tools in Garmin BaseCamp 4.6.2 software and magnetic declination was taken into account. The magnetic direction between the point of the excursion start and the GPS point recorded five seconds after the excursion start was measured (i.e. the initial outbound segment) and is defined here as azimuth A (***Figure 2A***). Azimuth B represents the magnetic direction of the owner relative to the dog at the turning point (***Figure 2A***). The magnetic direction of the initial inbound segment, azimuth C (denoted here as *compass run*), was determined by measuring the direction between the turning point and the point where the dog exhibited a > 20˚ deflection in track direction without an immediate return to its preceding track heading (***Figure 2A***). These criteria helped to omit short-lived track deviations often caused by obstacles (e.g. fallen trees, dense clusters of vegetation) and were applied to all tracks. A criterion for classifying the compass run as either north-south or east-west, was established by grouping runs into one of four sectors corresponding to a sector of ±45˚ of the cardinal compass axes, i.e. –north (316˚–45˚),–east (46˚–135˚),–south (136˚–225˚), or –west (226˚–315˚).

Return strategies

Based on preliminary evaluations from a subset of excursions, each inbound return was categorized into two distinct return strategies:

1. Tracking: The inbound return trajectory followed the outbound trajectory, i.e. the dog 'simply' followed its outbound track back to the owner (***Figure 2***). Here, the inbound return track is no more than 30 m from the outbound track at any point along the return path (***Figure 2***).
2. Scouting: A novel route of return was taken to the owner (i.e. dog was not following its outbound trajectory) (***Figure 2***). Here, the inbound and outbound trajectories were separated by more than 30 m (***Figure 2***).

In some cases, dogs exhibited a combination of return strategies, e.g. dogs began the inbound return trajectory using a tracking strategy and later changed to a scouting strategy, or vice versa (***Figure 2***). In these relatively rare situations (n = 50, 8.4 % of all excursions), strategies were divided into two separate tracks and the initial inbound segments (azimuth C) were measured for each strategy.

Importantly, the personnel responsible for identifying the spatial features of excursions (i.e. excursion start, outbound, turning and inbound trajectory, turning point and owner position, see Identifying excursion features) as well as partitioning tracks into return strategy type were unaware of the directional data (azimuths A, B, C). Conversely, personnel responsible for measuring directional data were unaware to which segments and strategies each measurement belonged. Therefore, the analysis of all directional data was carried out using a double-blind protocol.

Statistical analysis

Circular statistical analyses were carried out with Oriana 4.02 (Kovach Computing Services). Before evaluation, all directional responses were grouped by return strategy. Magnetic headings for azimuth A and azimuth B were treated as angular data. However, preliminary results for azimuth C revealed a strong bimodal response within individuals, and therefore, azimuth C was treated as axial data (***Batschelet, 1981***). The Rayleigh test was used for circular statistics to determine if distributions were indistinguishable from random at the $p<0.05$ significance level. To test for non-random orientation, all responses were evaluated at the individual level (i.e. measurements from excursion treated as an independent bearing) and at the group level by calculating mean directional response from each dog then calculating a grand mean vector. A Watson's U2 test was used to test for differences between distributions (***Batschelet, 1981***).

Non-circular data were analyzed using SAS System (version 9.4). Associations between inbound speed and return strategy, as well as homing efficiency and geomagnetic alignment (N-S or E-W) were tested using a multivariate General Linear Mixed Model (GLMM, PROC MIXED), with inbound speed or homing efficiency as a dependent variable. A homing efficiency index was expressed by calculating the ratio (in %) between the track length of the inbound trajectory (i.e. track length of dog between turning point and excursion start) and the direct distance (i.e. beeline) between the turning point and excursion start. Additional analyses (i.e. alignment or return strategies as dependent variables) were performed using a GLMM with PROC GLIMMIX for binary distributions. Link function was logit and the distribution of error terms was binomial in the GLMM. Since models with PROC GLIMMIX did not converge due to an effect with considerably larger classes (dog ID and/or breed), we applied the procedure with Method = Laplace (***Kiernan et al., 2012***).

Models were constructed by entering the predicted effects, i.e. return strategy for dependent variables, inbound speed and alignment (modelling the probability that geomagnetic alignment = N s); and dependent variable for homing efficiency index. Each model was checked with additional factors that could affect the model predictions (see ***Supplementary file 1C***- Table 3 for list of factors). Factors which did not contribute (i.e. factor significance $p>0.05$) were dropped from the model. Interaction terms were tested and all tests were treated as two-tailed distributions.

The effects used in the analyses were continuous variables and classes are listed in ***Supplementary file 1. C*** - Table 3. Where appropriate, variables were log-transformed to improve normality of residuals and to reduce skewness. All fitted models included the dog's identity as a random effect to account for the use of repeated measures across the same individuals.

Least-squares means (LSMEAN) were computed for each class and differences between classes were tested using a t-test. Associations between the dependent variable and time were estimated by fitting a random coefficient model using PROC MIXED (***Tao and Littell, 2002***). Predicted values of the dependent variable were calculated and plotted against the fixed effect with predicted regressions for each group. Where more than one value was plotted in the same position, a bubble plot was generated to represent the data.

To compare the probability of an event between two groups, an odds ratio was calculated (***Stokes et al., 2012***). Odds ratios greater than one imply that the event is more likely to occur in the first group, while an odds ratio less than one implies that the event is more likely to occur in the second group.

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Author contributions

Kateřina Benediktová, Conceptualization, Resources, Data curation, Formal analysis, Investigation, Visualization, Methodology, Writing - original draft; Jana Adámková, Investigation, Visualization, Methodology, Project administration; Jan Svoboda, Petra Nováková, Investigation; Michael Scott Painter, Formal analysis, Methodology, Writing - original draft, Writing - review and editing; Luděk Bartoš, Formal analysis, Visualization, Writing - original draft, Writing - review and editing; Lucie Vynikalová, Formal analysis, Visualization; Vlastimil Hart, Conceptualization, Supervision, Funding acquisition, Methodology, Writing - original draft, Project administration; John Phillips, Formal analysis, Writing - original draft, Writing - review and editing; Hynek Burda, Conceptualization, Formal analysis, Supervision, Funding acquisition, Validation, Visualization, Methodology, Writing - original draft, Project administration, Writing - review and editing

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Ethics

Animal experimentation: Permission from landowners and local game managers were obtained prior to entering each location, and searching and tracking methods were in accordance with the Czech national law and regulations for game management (§ 14 and § 15, Decree No. 244/2002, Ministry of Agriculture, Statue No. 449/2001, Game Management). The Professional Ethics Commission of the Czech University of Life Sciences in Prague has decided that according to the law and national and international rules, this study has not a character of an animal experiment and does not require a special permit.

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Additional files

Supplementary files

- Source data 1. Basic raw data used in calculations.

- Supplementary file 1. Information on subjects studied, parameters included in the analyses, and results of circular statistics. (A) Table 1 Information about dogs used in the study. Owner = initials of owner accompanying dog during walks, Age = age or age-range during the study period, N_{OUT} = number of outbound trajectories, N_{IN} = total number of inbound trajectories, N_T = number of inbound returns using a tracking strategy, N_S = number of returns using a scouting strategy. (B) Table 2 Factors in the final GLMMs for the dependent variables (in bold). a) probability for N-S alignment (±45˚) during the initial inbound segment (i.e. 'compass run'); b) probability for scouting strategy; c) efficiency of return; d) speed of inbound trajectory; e) inbound track length. (C) Table 3 Effects used in General Linear Mixed Models. (D) Table 4 Length parameters during different phases of the excursion (data from combined strategies are excluded). (E) Table 5 Circular analyses of individual ('raw') and grouped means for azimuth A, B and C during scouting and tracking strategies, and when a scouting strategy was used as the second return strategy (tracking used as a second return strategy not shown). Means were calculated by averaging directional headings for each dog, then calculating a grand mean from all individuals. Raw data were calculated by treating each azimuth as an independent bearing. Note that due to the bimodal preference found within individual dogs for azimuth C, these bearings were treated as axial data. See *Figures 6–8*. (F) Table 6 Axial analyses of azimuth C (=orientation of the compass run) partitioned into four groups to test for an influence of the owner on the orientation of the compass run during scouting strategy returns. Each analysis corresponds to the orientation of the compass run when the owner was located in one of four cardinal compass directions (±45˚) relative to the turning point. Therefore, owner positions relative to the turning point are: owner = magnetic ~ north (316˚–45˚),~east (46˚–135˚),~south (136˚–225˚), or ~west (226˚–315˚). All data are treated as independent bearings. (See *Figure 8*).

- Transparent reporting form

Data availability

The raw source data are provided as Source Data 1.

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