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Gehirnanatomie, "Life-History" und Kognition – Experimentelle komparative Studien an zwei Modellorganismen

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Für Henry und Evi

Inhaltsverzeichnis

I Eidesstattliche Erklärung

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II Originalarbeiten als Grundlage der kumulativen Habilitationsschrift

(nach Erwähnung im Text angeordnet)

1. **Cnotka** J, Güntürkün O, Rehkämper G, Gray RD, Hunt GR (2008) Extraordinary large brains in tool-using New Caledonian crows (*Corvus moneduloides*). *Neurosci. Lett.,* **433**, 241-245.
2. **Mehlhorn** J, Rehkämper G, Hunt GR, Gray RD, Güntürkün O (2010) Tool-making New Caledonian crows have large associative brain areas. *Brain Behav. Evol.*, **75**, 63-70.
3. Rehkämper G, Frahm HD, **Cnotka** J (2008) Mosaic evolution and adaptive brain component alteration under domestication on the background of evolutionary theory. *Brain Behav Evol*, **71**, 115-126.
4. **Cnotka** J, Möhle M, Rehkämper G (2008) Navigational experience affects hippocampus size in homing pigeons. *Brain Behav. Evol.*, **72**, 233-238.
5. **Mehlhorn** J, Haastert B, Rehkämper G (2010) Asymmetry of different brain structures in homing pigeons with and without navigational experience. *J. Exp. Biol.*, **213**, 2219-2224.
6. **Mehlhorn** J, Rehkämper G (2017) The orientation of homing pigeons (*Columba livia* f.d.) with and without navigational experience in a two-dimensional environment. *PLOS One,* 12 (11): e0188483. doi: 10.1371/journal.pone.0188483.
7. **Mehlhorn** J, Rehkämper G (2016) The influence of social parameters on the homing behavior of pigeons. *PLOS One*, **11(11): e0166572**. doi: 10.1371/journal.pone.0166572.

III Zusammenfassung

Neukaledonienkrähen (*Corvus moneduloides*) und Brieftauben (*Columba livia* f.d.) repräsentieren zwei Modellorganismen für die Neuro- und Kognitionswissenschaften. Beide Arten zeigen spezifische kognitive Fähigkeiten. Bei den Neukaledonienkrähen ist es die Fähigkeit zur Werkzeugherstellung und deren Gebrauch, wobei sie auch in der Lage sind, kausale Zusammenhänge zu erkennen. Bei den Brieftauben sind es herausragende Orientierungs- und Navigationsfähigkeiten im Sinne einer "spatial cognition“.

In den vorliegenden Arbeiten konnte erstmalig die Gehirnarchitektur beider Arten morphometrisch im Detail erfasst werden. Parallel dazu wurde gezeigt, dass beide Arten in ihren kognitionspezifischen Hirnarealen volumetrisch exakt erfassbare Größenanpassungen aufweisen. Bei den Neukaledonienkrähen zeigte sich dies vor allem in relativen Vergrößerungen assoziativer Hirnareale wie dem Mesopallium und dem striatopallidalen Komplex. Die Brieftauben zeigten eine relative Vergrößerung des Hippocampus als Kernstück für die Verarbeitung räumlicher Informationen und des Bulbus olfactorius als sinnesverarbeitende Struktur, dessen Informationen für die Orientierung genutzt werden. Umfangreiche Experimente mit den Brieftauben belegten einen eindeutigen Einfluss von (Navigations-) Erfahrung auf den Hirnbau, und zwar insbesondere auf den Hippocampus. Tiere ohne Navigationserfahrung weisen einen kleineren Hippocampus auf als Tiere mit Navigationserfahrung. Zudem ist das Gehirn von Tieren mit Navigationserfahrung stärker lateralisiert, das heißt, es gibt mehr (volumetrische) Rechts-Links-Unterschiede. Das spricht für eine effizientere Verarbeitungsweise, da neuronale Schaltkreise nur in einer Hemisphäre ablaufen und unnötige Verdoppelungen sowie mögliche Interferenzen reduziert oder sogar vermieden werden. Bei experimentellen Untersuchungen in der Skinner-Box zum Einfluss von Erfahrung auf die Orientierungsfähigkeit im zweidimensionalen Raum zeigten auch hier Tiere ohne Navigationserfahrung prinzipiell schlechtere (Orientierungs-) Leistungen, insbesondere bei monokularen Sichtbedingungen. Die letzte Untersuchung machte deutlich, dass die Interpretation von realen Navigationsleistungen in Form von Flugdaten kritischer erfolgen muss als bisher angenommen, da sich ein deutlicher Einfluss von sozialen Parametern wie Geschlecht, Paarungs- oder Brutstatus auf die Heimkehrmotivation und damit Flugeffizienz zeigte. Zusammenfassend konnten umfangreiche neuroanatomische Vergleiche zwischen Neukaledonienkrähen und Brieftauben angestellt werden, die kognitions- bzw. verhaltensspezifische Anpassungen belegten. Die Untersuchungen zur Plastizität und Lateralisation des Gehirns zeigten im weiteren einen deutlichen Einfluss der individuellen „Life-History“ sowohl auf die Anatomie des Gehirns als auch auf die kognitive Leistungsfähigkeit der jeweiligen Individuen.

„Die großen Ideen kommen auf Taubenfüßen daher“

Friedrich Nietzsche

IV Einleitung

Vögel (*Aves*) repräsentieren eine ähnlich erfolgreiche Klasse der Wirbeltiere wie die Säugetiere und sind wie diese weit verbreitet sowie in alle ökologischen Großräume eingedrungen. Neuroanatomisch fällt bei beiden Klassen auf, dass im Vergleich zu anderen rezenten Vertebraten schon makroskopisch das Telencephalon die anderen Hirnteile dominiert. Die vergleichende Betrachtung des Hirnbaus bei Säugern und Vögeln wurde bereits Anfang des 20. Jahrhunderts u.a. von Edinger (1903) und Kappers et al. (1936) systematisch in Angriff genommen. Kuhlenbeck (1967-1978) hat diese Erkenntnisse zusammengetragen, ergänzt und eine stringente, klassenübergreifende Nomenklatur vorgeschlagen. Nieuwenhuys et al. (1998) bieten in einem dreibändigen Werk einen aktualisierten Überblick.

Die frühen Autoren betonten bezüglich der Säuger und Vögel vor allem die Verschiedenheit, während nachfolgende Forschungen auch zahlreiche Ähnlichkeiten aufzeigten (Karten, 1969; Rehkämper und Zilles 1991; Rehkämper et al., 1991a).

Nachfolgend wurden diese Arbeiten durch Verhaltensstudien ergänzt und um funktionelle Aspekte erweitert. Hierbei waren und sind auch heute noch vor allem telencephalonbasierte Verhaltensweisen von Interesse und ein Forschungsfeld der kognitiven Neurowissenschaften, das sehr viel Aufmerksamkeit auf sich gezogen hat, rückt Vergleiche zwischen verschiedenen Arten respektive ihren kognitiven Fähigkeiten und deren neuronalen Grundlagen in den Vordergrund. Besonders interessant sind hierbei Vögel, die sich in ihren kognitiven Fähigkeiten kaum von Säugern unterscheiden, deren Hirnbau aber ganz anders organisiert zu sein scheint, so dass in den letzten Jahrzehnten immer mehr Vogelmodelle in den Fokus der Wissenschaft gerückt sind. Die hohen kognitiven Fähigkeiten von diversen Papageienarten werden dabei als schon fast vergleichbar mit denen von Primaten angesehen. Auch die Herstellung und der Gebrauch von Werkzeugen bei einigen Vertretern der Rabenvögel (*Corvidae*) stehen diesbezüglichen Aktivitäten der Primaten in nichts nach und werden als Ausdruck einer kognitiven Potenz gesehen [Hunt, 1996; Pepperberg, 2002;

Emery und Clayton, 2004; Clayton und Emery, 2015]. Dies wirft die Frage auf, ob sich ähnliche höhere kognitive Fähigkeiten evolutionär auf zwei völlig unterschiedlichen Arten entwickelt und in einem unterschiedlichen Hirnaufbau ihr strukturelles Korrelat gefunden haben.

Die Unterschiede im Hirnbau von Vögeln und Säugetieren sind bemerkenswert, wobei als auffälligstes Merkmal sicherlich das Fehlen einer mit dem Cortex vergleichbaren laminierten Struktur bei Vögeln anzusehen ist. Aufgrund dessen wurde lange Zeit die Ansicht vertreten, dass das Vorderhirn der Vögel aus extrem vergrößerten und komplexen Basalganglien („Striatum") bestehe [Ariëns-Kappers et al., 1967]. Dies passte zu der damaligen Annahme, dass Säuger ein weitaus komplexeres, flexibleres Verhaltensrepertoire aufweisen sollten, wofür nach damaliger Meinung das Vorhandensein eines Neocortex vonnöten sei. Mittlerweile ist die Forschung am Vogelhirn weit fortgeschritten und es ist bewiesen, dass der Großteil des Telencephalons neurochemisch, hodologisch und funktionell mit dem Neocortex, dem Claustrum und dem Corpus amygdaloideum der Säuger vergleichbar ist und nur ein kleiner Teil des aviären Telencephalons bzw. Subpalliums direkt mit dem Striatum der Säuger verglichen werden kann [z.B. Reiner et al., 1984; Shimizu und Karten, 1993; Güntürkün, 1997b]. Aufgrund dieser Erkenntnisse kam es bereits 2004 zu einer Überarbeitung der bestehenden Nomenklatur des Vogelhirns durch das so genannte *„Avian Brain Nomenclature Consortium"*, was zu einer signifikant geänderten Terminologie geführt hat [Reiner et al, 2004; The Avian Brain Nomenclature Consortium, 2005]. Mittlerweile sind erstaunlich viele Ähnlichkeiten zwischen dem aviären Pallium und dem Neocortex der Säuger aufgedeckt worden. Es scheint, dass diese Parallelen evolutionär gesehen aus einer Mischung aus homologen Elementen und analogen bzw. konvergenten Merkmalen bestehen [Güntürkün und Bugnyar, 2016].

Für das tägliche Überleben sind sowohl Menschen als auch Tiere auf eine schnelle Bewertung und flexible Nutzung verschiedenster Umweltreize und Informationen angewiesen. Das beinhaltet auch die Fähigkeit, sich auf wechselnde Umweltbedingungen einzustellen, kontextabhängige Entscheidungen zu treffen und in sozialen Situationen zu lernen. Kognitive Eigenschaften wie Wahrnehmung und Aufmerksamkeit, Erinnerung und Lernen, Problemlösen, Kreativität und Vorstellungskraft, Planen und Orientierung sind der Schlüssel zu der weiten Verbreitung der Säugetiere und letztendlich auch der Vögel (Anderson, 2013). Die Neurowissenschaften beschäftigen sich schon lange mit der Analyse von kognitiven Prozessen im Gehirn von Vögeln, jedoch gibt es nach wie vor Unklarheiten und offene Fragen, auch was die gängigen Vogelmodelle angeht. Zurzeit wird bei Untersuchungen zu spezifischen Aspekten des Lernens und der Kognition in Zusammenhang mit der relevanten Neurobiologie hauptsächlich mit drei Vogelmodellen gearbeitet: mit Singvögeln wie z.B. Zebrafinken, sowie mit Haushühnern und verschiedenen Haustauben. Die Taube gilt hierbei vor allem bei Studien zum Verständnis von Lernvorgängen an sich, zum räumlichen Gedächtnis ("spatial cognition") und im Speziellen zur visuellen Diskriminierung und Navigation als das Modell der Wahl [Clayton und Emery, 2015]. Wenn allerdings komplexe kognitive Fähigkeiten untersucht werden sollen und evtl. noch ein Vergleich mit Menschen oder nicht-menschlichen Primaten angestrebt wird, ist die Nutzungsmöglichkeit der oben genannten Modelle begrenzt. Hier zeigte sich in den letzten Jahren, dass sich vor allem Vertreter der Rabenvögel (*Corvidae*) als Modell eignen würden. Allerdings herrscht hier noch großer Forschungsbedarf, vor allem was die Neurobiologie angeht.

Die hier vorgelegten Arbeiten haben einen Beitrag zu dieser Thematik geleistet, indem zwei verschiedene Vogelmodelle mit sehr unterschiedlichen kognitiven Verhaltensweisen hinsichtlich Gehirnarchitektur sowie im Hinblick auf ihr Verhalten untersucht und miteinander verglichen wurden. Zum einen wurde mit einem Modelltier gearbeitet, das für diese Fragen sehr zentral geworden ist: der Haustaube, genauer der Brieftaube (*Columba livia* f.d.). Zum anderen wurde die neukaledonische Geradschnabelkrähe oder Neukaledonienkrähe (*Corvus moneduloides)* untersucht, deren bemerkenswerte Fähigkeiten in der Werkzeugherstellung bzw. dem Werkzeuggebrauch sie zu einem viel beachteten Forschungsobjekt für das Verständnis höherer kognitiver Leistungen bei Vögeln gemacht haben (z.B. Hunt, 1996). Dies hat sogar zu einer gewissen medialen Berühmtheit einzelner Exemplare geführt („Betty“ aus Oxford, z.B. Weir et al., 2002). Die eigenen Untersuchungen an Brieftaube und Krähe zielen zum einen darauf, bisherige Befunde innerhalb dieser Arten zu komplementieren. Zum anderen sollen in einem komparativen neuroanatomischen Ansatz Parallelen und Unterschiede zwischen den Arten herausgearbeitet werden, um zu einem differenzierten Verständnis der Bedeutung der Gehirnanatomie für spezifische höhere kognitive Fähigkeiten zu gelangen.

Dabei wurden auch Untersuchungen zur Plastizität und Lateralisation des Gehirns durchgeführt, die Rückschlüsse auf den Zusammenhang von Hirnbau und Hirnfunktion erlauben. Diese Untersuchungen wurden unter besonderer Berücksichtigung der individuellen Erfahrung („Life-History“) der Tiere durchgeführt, um den potentiellen Einfluss auf den Hirnbau und die Hirnfunktion zu überprüfen und zu präzisieren.

Die Neukaledonienkrähe gehört zur Ordnung der Sperlingsvögel oder Singvögel (*Passeriformes*) und hier zu der Familie der Rabenvögel (*Corvidae*). Innerhalb der Klasse der Vögel zeichnen sich die Corviden vor allem durch ihre hohen kognitiven Fähigkeiten und ihre flexiblen Verhaltensweisen aus [z.B. Rehkämper et al., 1991; Iwaniuk und Hurd, 2005; Güntürkün und Bugnyar, 2016] und werden bisweilen sogar als ideales Modelltier für menschliches Verhalten bzw. menschliche Kognition angesehen [Clayton und Emery, 2015]. Bei der Neukaledonienkrähe, die zu dieser Familie gehört, wurden erstmals herausragende Fähigkeiten in der Werkzeugherstellung und im Werkzeuggebrauch beobachtet, die es den Tieren möglich machen, an Futterquellen zu gelangen, die sonst unerreichbar geblieben wären [Hunt, 1996; Hunt and Gray, 2003, 2004a]. Diese Vögel sind in der Lage, eine ganze Bandbreite an Werkzeugen sowohl aus Stöcken als auch aus Blättern herzustellen [Hunt and Gray, 2002, 2003, 2004b]. Selbst ihnen unbekanntes Material wie Draht können sie für die Herstellung von feinem Werkzeug zurechtbiegen [Weir et al., 2002]. Beobachtet wurde auch, dass sie "Metawerkzeuge" benutzen, d.h. Werkzeuge, die ihnen helfen, an andere, besser geeignete Werkzeuge zu gelangen [Taylor et al., 2007]. Zudem sind sie in der Lage, kausale Zusammenhänge zu erfassen [Taylor et al., 2009]. Diese Fähigkeiten sind nach Meinung vieler Autoren durchaus mit den Fähigkeiten von Primaten vergleichbar [Taylor et al., 2009; Emery and Clayton, 2004; Emery, 2006].

Das zweite Modelltier, das im Rahmen der hier vorgelegten Untersuchungen näher betrachtet werden soll, ist die Brieftaube. Die heutige Brieftaube ist das Ergebnis jahrhundertelanger, intensiver Zuchtbemühungen auf Ausdauer, Schnelligkeit, und vor allem auf exzellentes Heimfindevermögen. Letzteres ermöglicht den Tieren, nach der Auf- bzw. Freilassung an von ihnen unbekannten

Orten, die mehr als 1000 km entfernt liegen können, wieder zum heimischen Schlag zurückzufinden. Diese Fähigkeit macht diese Tiere zu idealen Forschungsmodellen, z.B. zu Themen der Domestikationsforschung und der Verhaltensforschung. Hier ist vor allem hervorzuheben, dass Erkenntnisse zu ihrem Heimfindevermögen auch Rückschlüsse auf das Navigationsvermögen von Zugvögeln erlauben bzw. zu Orientierungsphänomenen überhaupt. Zudem hat sich die Taube durch ihre hohe Lebenserwartung, gekoppelt mit hoher Lernbereitschaft und Frustrationstoleranz, in den letzten Jahren zu einem der wichtigsten Vogelmodelle der Kognitionsforschung und der Neurowissenschaften entwickelt. Sie liefert durch ihre hohe kognitive Leistungsfähigkeit und ihr hoch entwickeltes visuelles System nicht nur Einblicke in die experimentelle Psychologie (und hier v.a. in die visuelle Kognition), sondern bietet auch grundlegende Einblicke in vielfältige Themenbereiche, die z.T. sogar eine Übertragung auf den Menschen erlauben. Diese Übertragbarkeit begründet sich auf zahlreichen neueren Untersuchungen, die zeigen, dass das Telencephalon von Säugern und Vögeln homolog ist, und dass die neuronalen Mechanismen von Lernen und Handlungssteuerung im Vogelhirn denen im Säugerhirn stark ähneln.

Im Gegensatz zu Zugvögeln, welche zwischen weit entfernten, aber stets gleichen Räumen pendeln, besitzt die Felsentaube als wildlebende Stammform der Brieftauben die angeborene Fähigkeit, aus beliebigen Gebieten und Richtungen zum Nistplatz zurückzufinden. Diese Fähigkeit hat sich der Mensch schon früh zu Nutze gemacht und die Taube als Informationsübermittler eingesetzt. Die Taubenpost gilt als älteste Form der Flugpost und wurde seit dem Altertum rege genutzt. Sei es in der Antike durch Julius Cäsar, im Mittelalter durch die Kreuzritter oder auch während des Deutsch-Französischen Krieges (1870/1871), als Brieftauben (als Teil der so genannten Pariser Ballonpost) Nachrichten aus dem unbesetzten Frankreich nach Paris überbrachten [Haag-Wackernagel, 1998]. Auch wurden in beiden Weltkriegen noch Brieftauben zur Nachrichtenübermittlung mit sehr hoher Erfolgsquote eingesetzt. Ein Technisches Merkblatt zum "Einweg-Mikrokurier Bft Suisse" verdeutlicht die Vorteile von Brieftauben im militärischen Bereich. Hier ist von einem "elektronisch absolut nicht zu ortenden, selbstreproduzierenden Kleinflugkörper auf biologischer Basis mit festprogrammierter automatischer Rückkehr aus beliebigen Richtungen und Distanzen zur Übermittlung von Daten" die Rede

[Lipp, 1980]. Die Schweizer Armee unterhielt bis ins Jahr 1994 einen Brieftaubendienst, die Volksrepublik China sogar noch länger.

Im Gegensatz zu anderen Rassetauben, bei denen vornehmlich auf das Aussehen hin gezüchtet wird, steht bei den Brieftauben allein die Leistung im Vordergrund. Eine lange und strenge Selektion führte zu immer besseren Navigationsfähigkeiten, gekoppelt mit einer starken Heimkehrmotivation, großer körperlicher Kraft und gesteigerter Ausdauer. Dies führte dazu, dass heute das Heimfindevermögen der Brieftauben das der Felsentaube, ihrer wilden Stammform, mittlerweile weit übersteigt, vor allem wenn es um das erfolgreiche Absolvieren größerer Distanzen geht [Alleva et al., 1975; Visalberghi et al., 1978].

Es ist mittlerweile anerkannt, dass das Heimfindevermögen der Brieftaube auf einer genetischen Prädisposition, multimodalem Lernen und einer ausgeprägten Fähigkeit zur räumlichen Wahrnehmung basiert, und dass sie eine Vielzahl von Informationen in einer Weise miteinander verbindet, die man intelligent nennen könnte [Lipp, 1983; Wallraff, 2001]. Zu den bekannten Mechanismen, die bei der Orientierung und Navigation eine Rolle spielen, zählen u.a. die Nutzung eines Sonnenkompass und des Erdmagnetfeldes sowie die Einbeziehung olfaktorischer und visueller Informationen. Wahrscheinlich spielen auch Parameter wie Motivation und Erfahrung eine nicht unerhebliche Rolle [Papi et al. 1974; Schmidt-König, 1990; Bingmann, 1993, Mehlhorn und Rehkämper, 2009]. Es ist immer noch unklar, wann und inwiefern alle bisher bekannten Faktoren miteinander agieren. Die Effizienz hängt von Gegebenheiten wie den Charakteristika der Umgebung ihres Heimatschlags, der entsprechenden Auflassorte, dem Gebiet zwischen Auflassort und Heimatschlag und letztendlich auch vom Einzeltier mit seiner Erfahrung und speziellen Lebensgeschichte ab.

V Zielsetzung und Aufbau der Arbeit

Die vorliegende Arbeit untersucht die Struktur des Gehirns von Neukaledonienkrähen (*Corvus moneduloides)* und Brieftauben (*Columba livia* f.d*.)* in seinen Wechselbeziehungen mit den artspezifischen kognitiven Fähigkeiten. Dabei nehmen die Studien zu den Struktur-Funktionsbeziehungen im Gehirn der Brieftaube einen besonders breiten Raum ein, weil sich der erkenntnistheoretische Wert der Studien an diesen Tieren in Bezug auf grundlegende Fragen der Neurowissenschaften und auch der Ethologie als besonders groß erwiesen hat.

Bei den Untersuchungen wurde eine multimodale Herangehensweise gewählt, die sowohl neuroanatomische als auch verhaltensbiologische Untersuchungen beinhaltet. Bei der Neukaledonienkrähe wurde erstmalig die Neuroanatomie des Gehirns morphometrisch untersucht und in einen (allometrischen) Vergleich mit anderen Vogelarten gestellt. Bei der Brieftaube wurden zum einen neuroanatomische Untersuchungen zum Hirnbau durchgeführt und in Relation zu anderen Taubenrassen gesetzt. Zum anderen wurde der Einfluss von Erfahrung auf die quantitative Hirnzusammensetzung erfasst und in kausalen Zusammenhang mit der Fähigkeit der Tiere zur räumlichen Kognition gesetzt. Erstmalig war auch der Einfluss von Erfahrung auf Hemisphärenunterschiede (Lateralisation) Gegenstand von Untersuchungen sowie der Einfluss von sozialen Parametern auf die räumliche Kognition.

Basierend auf den Ergebnissen konnte abschließend ein interspezifischer Vergleich zwischen Krähen und Tauben angestellt werden und es konnten Schlussfolgerungen zu den Wechselbeziehungen zwischen dem Gehirn und diversen kognitiven Fähigkeiten gezogen werden.

VI Ergebnisse und Diskussion

VI.1 Hirnbau und Kognition der Neukaledonienkrähe (*Corvus moneduloides)*

Wie einleitend schon erwähnt, wurde in den letzten Jahrzehnten immer deutlicher, dass die traditionelle Einschätzung von Vögeln als instinktgesteuerte Tiere mit geringen kognitiven Fähigkeiten revidiert werden muss. Als Paradebeispiel für Vögel mit hohen kognitiven Fähigkeiten gelten seit langem Papageienvögel (Ordnung *Psittaciformes*), die z.B. auch neben der Entwicklung von Problemlösungsstrategien ein komplexes und interaktives Sozialverhalten zeigen [Pepperberg, 2002]. Innerhalb der Ordnung der *Passeriformes* zeichnet sich vor allem die Familie der Corviden durch flexibles Verhalten und bemerkenswerte Lerneigenschaften aus [Schloegl et al., 2009]. In der Vergangenheit wurde bereits gezeigt, dass, ähnlich wie bei Säugetieren, hohe kognitive Fähigkeiten mit einem größeren Gehirn assoziiert sind [Portmann, 1946, Harvey & Krebs, 1990, Lefebvre et al., 1997; Rehkämper et al., 2001; Iwaniuk et al., 2004].

Von der Neukaledonienkrähe (*Corvus moneduloides*, Abb. 1) ist schon seit längerem bekannt, dass sie die kognitive Leistung der Werkzeugherstellung und dessen Gebrauch beherrscht.

Abb. 1. Habitus einer Neukaledonienkrähe (*Corvus moneduloides*) mit einem selbsthergestellten pflanzlichen Werkzeug. Verwendung der Abbildung mit freundlicher Genehmigung des Elsevier Verlages (Cnotka et al., 2008b).

Trotzdem fehlten bislang Untersuchungen zum Hirnbau bzw. zur Neuroanatomie dieser Art. Um diese Lücke zu schließen, wurden Neukaledonienkrähen in ihrem natürlichen Habitat in Neukaledonien gefangen und vor Ort ihre Gehirne entnommen. Die weitere Aufarbeitung erfolgte an der Universität Düsseldorf. Als erstes wurden die neuen Daten für einen Vergleich zwischen den Hirngewichten von Neukaledonienkrähen und vier anderen Arten der Ordnung *Passeriformes* genutzt. Letztere stammten aus der arbeitsgruppeneigenen Hirnsammlung und waren in gleicher Weise bestimmt worden [Cnotka et al., 2008, **Publikation 1**]. Dann wurden zum Vergleich noch Hirn- und Körpergewichte aus einem umfangreicheren Datensatz von Portmann [1946] herangezogen. Dieser umfasst 140 verschiedene Vogelarten, davon sieben aus der Familie der Corviden. Ziel war, zu testen, ob die kognitiven Fähigkeiten der Neukaledonienkrähe mit der Gesamthirngröße korrelieren.

Für den Vergleich der Hirngewichte wurde mit einer allometrischen Methode gearbeitet, die Unterschiede in der Hirngröße unabhängig von Unterschieden in der Körpergröße zeigt. Diese Methode wurde von Snell [1892] vorgestellt, ist seither sehr stark verfeinert worden und hat sich als außerordentlich aussagekräftig erwiesen [Dubois, 1897; Harvey, 1988; Stephan et al. 1986; Baron et al., 1996].

Kernstück der Methode ist, den Einfluss der Körpergröße auf die Hirngröße mathematisch zu bestimmen. Dabei sollte, um eine geeignete Bezugsbasis herzustellen, die Bandbreite im Körpergewicht der zu vergleichenden Tiere möglichst groß sein, was in unseren Untersuchungen gegeben war. Die Körpergewichte und die Hirngewichte wurden in doppelt logarithmischer Form aufgetragen und anschließend eine lineare Regressionsgerade durch die Datenpunkte aller Tiere berechnet. Aufgrund der Funktionsgleichung dieser errechneten Regressionsgeraden konnten Encephalisationsindices kalkuliert werden, die den Abstand jedes individuellen Wertes von der Regressionsgerade beschreiben [Stephan et al., 1988]. Jeder Wert auf der Regressionsgeraden würde einem Encephalisationsindex von 1 entsprechen, so dass z. B. ein Index von 2 bedeutet, dass das Gehirn doppelt so groß ist, wie es aufgrund der Regressionsgerade zu erwarten wäre. Jerison [1973] hat diese Differenz als "extrabrain" bezeichnet und als Indikator z.B. von kognitiven Fähigkeiten interpretiert. Diese Encephalisationsindices der verschiedenen Vogelarten wurden in einem letzten Schritt gemittelt und statistisch miteinander verglichen.

Bei solchen Vergleichen sollten phylogenetische Verwandtschaften innerhalb der Klasse *Aves* berücksichtigt werden. Insgesamt wurden deshalb drei Regressionsanalysen durchgeführt. Die erste erfolgte innerhalb der Ordnung *Passeriformes* mit den vier Referenzarten Haussperling (*Passer domesticus*), Elster (*Pica pica*), Eichelhäher (*Garrulus glandarius*) und Rabenkrähe (*Corvus c. corone*). Für die zweite und dritte Analyse wurde der Datensatz von Portmann (1947) genutzt, der sich aus den Mittelwerten von den Hirn- und Körpergewichten 140 verschiedener Vogelarten zusammensetzt. Hier wurde zuerst geprüft, wie sich die Hirngröße der Neukaledonienkrähe im Vergleich mit Vögeln im Allgemeinen verhält. In der dritten Analyse wurden nur die Daten der sieben Arten der Familie der Corviden aus dem Datensatz von Portmann genutzt.

Die Neukaledonienkrähen stachen in mehrerer Hinsicht hervor. Zum einen wiesen sie einen signifikant größeren Encephalisationsindex auf als alle anderen im Vergleich vorliegenden passeriformen Arten (Abb. 2).

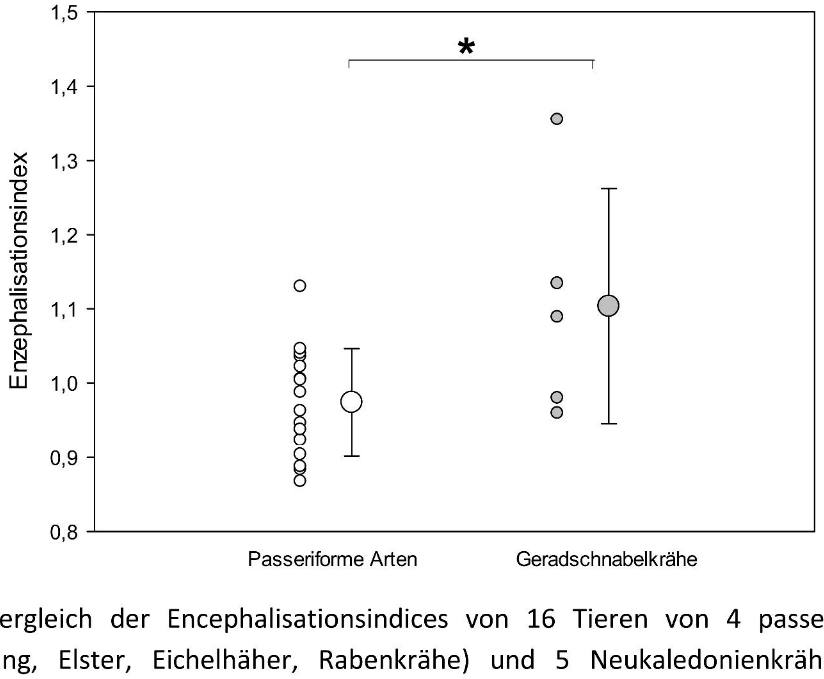


Abb. 2. Vergleich der Encephalisationsindices von 16 Tieren von 4 passeriformen Vogelarten (Haussperling, Elster, Eichelhäher, Rabenkrähe) und 5 Neukaledonienkrähen. Einzeldaten mit Mittelwert und Standardabweichung, rechts jeweils der Fehlerbalken, *p=0.017. Verwendung der Abbildung mit freundlicher Genehmigung des Elsevier Verlages (Cnotka et al., 2008b).

Zum anderen zeigen sie im Vergleich mit den 140 anderen Vogelarten das vierthöchste Hirngewicht. Nur der Gelbbrustara (*Ara arauna)*, der Grünflügelara *(Ara chloroptera)* und der Schwarzspecht *(Dryocopus martius)* weisen größere Encephalisationsindices auf (Abb. 3).

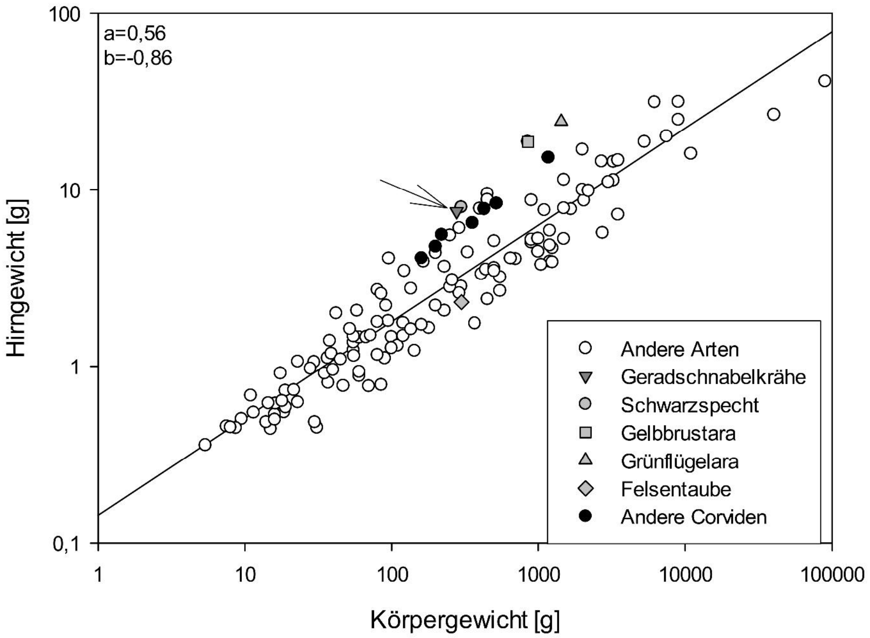


Abb. 3. Hirngewicht und Körpergewicht von 141 verschiedenen Vogelarten doppelt logarithmisch aufgetragen. Ein Symbol kennzeichnet eine Art. Der Pfeil weist auf das Symbol der Neukaledonienkrähe. Da Tauben das gängigste Vogelmodell in verhaltens- und neurobiologischen Studien darstellen, ist die Felsentaube ebenfalls markiert. Verwendung der Abbildung mit freundlicher Genehmigung des Elsevier Verlages (Cnotka et al., 2008b).

Portmanns Datensatz beinhaltet die sieben Corviden Kolkrabe (*Corvus corax*), Rabenkrähe (*Corvus c. corone*), Saatkrähe (*Corvus frugilegus*), Elster (*Pica pica*), Dohle (*Corvus monedula*), Alpenkrähe (*Pyrrhocorax pyrrhocorax*) und Eichelhäher (*Garrulus glandarius*). Setzt man die Daten der Neukaledonienkrähen in Beziehung dazu, so zeigen sie auch hier signifikant den höchsten Encephalisationsindex.

Die Studie Cnotka et al. (2008) gibt erstmalig einen Einblick in die Neuroanatomie der Neukaledonienkrähe. Es konnte gezeigt werden, dass die relative Hirngröße dieser Tiere größer als bei anderen Vögeln ist und nur von einer kleinen Anzahl nicht-passeriformer Arten übertroffen wird. Demzufolge sind die außergewöhnlichen Fähigkeiten dieser Tiere mit einem der höchsten

Encephalisationswerte gepaart, die bisher im gesamten Vogelreich festgestellt werden konnten. Große Gehirne resultieren in der Regel daraus, dass es zu einem selektiven, mosaikartigen relativen Wachstum bestimmter Hirnareale kommt [Rehkämper et al., 2001; Iwaniuk et al., 2004]. Bei nicht-passeriformen Arten, wie z.B. den Kolibris, ist das Gesamthirn disproportional vergrößert, was aber auf eine einseitige progressive Vergrößerung des Cerebellums zurückzuführen ist [Rehkämper et al. 1991b]. Meistens kann jedoch beobachtet werden (auch bei nicht-passeriformen Papageien und bei vielen passeriformen Arten), dass eine höhere Encephalisation auf ein verstärktes Wachstum des telencephalen Palliums zurückzuführen ist [Rehkämper et al., 1991, 2001; Iwaniuk et al., 2004; Sultan, 2005]. Sowohl bei Papageien als auch bei Corviden im Allgemeinen wurde bereits gezeigt, dass die hohen Encephalisationswerte auf Vergrößerungen der assoziativen Vorderhirnareale wie dem Mesopallium und Nidopallium beruhen, die in kognitive Funktionen wie Flexibilität, Arbeitsgedächtnis, Kontextintegration oder Problemlösung eingebunden sind [Rehkämper et al., 1991; Güntürkün, 2005; Iwaniuk und Hurd, 2005]. Die außergewöhnlichen Fähigkeiten der Neukaledonienkrähen in der Werkzeugherstellung und dem Werkzeuggebrauch sind einerseits sicher Ausdruck eines gewissen motorischen Geschicks, werden aber hauptsächlich als kognitive Leistungen diskutiert. Sie legen nahe, dass die großen Gehirne dieser Tiere auf Vergrößerungen in telencephalen Hirnarealen beruhen, die mit kognitiven Leistungen verbunden werden.

Um mögliche Korrelationen zwischen der Encephalisation und kognitiven Fähigkeiten konkreter zu untersuchen, war der nächste Schritt eine komparative Analyse der verschiedenen Hirnareale, darunter auch kognitionsrelevanten Bereichen. Dazu wurde in der folgenden Arbeit [Mehlhorn et al., 2010; **Publikation 2**] eine Größenbestimmung von 15 Hirnarealen vorgenommen und diese mit drei anderen passeriformen Arten (Rabenkrähe (*Corvus c. corone*), Eichelhäher (*Garrulus glandarius*) und Haussperling (*Passer domesticus*)) verglichen. Da die Größe des Nidopallium als bester Hinweis für den Werkzeuggebrauch gilt [Lefebvre et al., 2002], war zu erwarten, dass es im Vergleich zu den anderen Arten, bei denen allesamt bisher kein Werkzeuggebrauch beobachtet wurde, relativ größer ist. Ähnlich war die Erwartungshaltung bezüglich des Mesopalliums, dessen Größe als Hinweis für innovatives Verhalten und allgemeine Flexibilität bzw. Anpassungsfähigkeit dienen kann [Timmermanns et al., 2000]. Ebenso wurde untersucht, ob andere assoziative Hirnareale, wie z.B. der striatopallidale Komplex, bei Neukaledonienkrähen vergrößert sind.

Für die Größenbestimmung der Hirnareale wurden von allen Gehirnen Schnittserien angefertigt, sofern sie nicht schon vorlagen, und an allen Zellkörperfärbungen vorgenommen (Versilberung nach Gallyas, 1971). An den Schnittserien wurden folgende Strukturen vermessen/bestimmt und unter Einbeziehung eines individuellen Schrumpfungsfaktors auf das Frischvolumen hochgerechnet: Hyperpallium apicale, Hyperpallium densocellulare, Mesopallium, Nidopallium (inklusive Nucleus basalis und Feld L), Arcopallium (inklusive Nucleus taeniae amygdalae und Teile des Tractus occipitomesencephalicus), Entopallium, der striatopallidale Komplex (inklusive Globus pallidus, Striatum mediale, Striatum laterale und Tuberculum olfactorium), Septum, Hippocampus, Bulbus olfactorius, Tegmentum, Cerebellum, Tectum opticum, Tractus opticus und Diencephalon (Abb. 4).

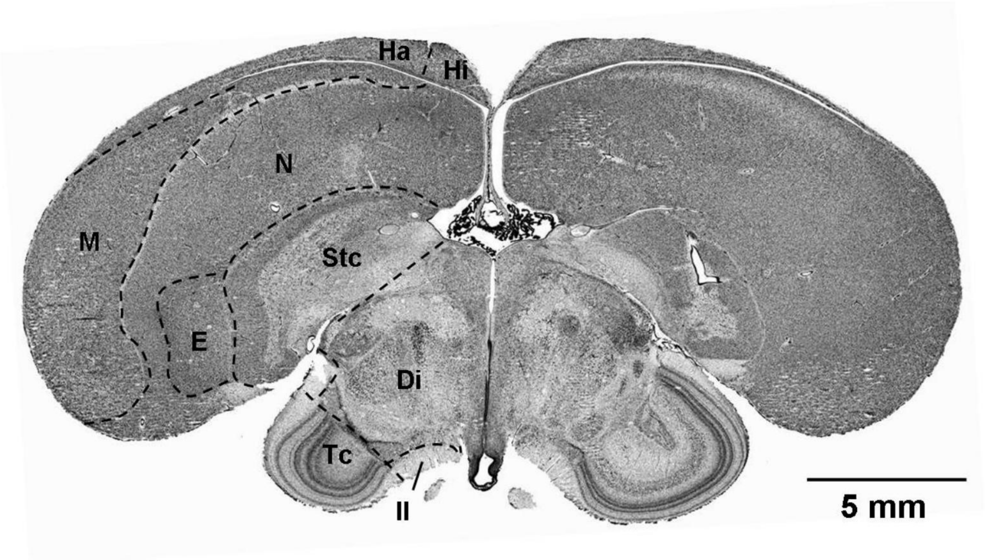


Abb. 4. Frontalschnitt durch das Gehirn einer Neukaledonienkrähe zur Darstellung einiger Hirnreale. Di=Diencephalon, E=Entopallium, Ha=Hyperpallium apicale, Hi=Hippokampus, M=Mesopallium, N=Nidopallium, Stc=Striatopallidaler Komplex, Tc=Tectum opticum, II=Tractus opticus. Versilberung nach Gallyas. Verwendung der Abbildung mit freundlicher Genehmigung des Karger Verlages (Mehlhorn et al., 2010).

Wie schon in der vorangegangenen Arbeit wurde für die Auswertung mit der allometrischen Methode gearbeitet. Ebenso wurden wieder auf Grundlage von Regressionsanalysen Indices errechnet, allerdings diesmal für jede einzelne vermessene Hirnstruktur. Auch hier galt wieder, dass jeder Wert auf der Regressionsgeraden einem Index von 1 entsprechen würde, so bedeutet z. B. ein Index von 2, dass diese Struktur doppelt so groß ist, wie es aufgrund der Regressionsgerade zu erwarten wäre. Um unsere Hypothese zu überprüfen, dass sich der Werkzeuggebrauch und andere kognitiven Fähigkeiten in der Größe von assoziativen Vorderhirnarealen wiederspiegeln, wurde als erstes ein Vergleich mit den zusammengefassten Daten der Rabenkrähen, Eichelhähern und Hausspatzen durchgeführt, welche alle als geeignete Repräsentanten der Ordnung *Passeriformes* angesehen werden können und zudem alle relativ große Gehirne aufweisen [Portmann, 1947; Rehkämper et al., 1991; Boire und Baron, 1994]. Dieser Vergleich diente dazu, die Stellung der Neukaledonienkrähe innerhalb der Ordnung *Passeriformes* zu bestimmen. Ein alternativer Vergleich der Neukaledonienkrähe mit jeder Art separat war aufgrund der geringen Tierzahl der Eichelhäher (n=2) und Sperlinge (n=4) nicht möglich. Allerdings wurde ein direkter Vergleich mit der Rabenkrähe angestellt, um auszuschließen, dass Hirnstrukturvergrößerungen der Neukaledonienkrähe auf ein generelles Charakteristikum der Gattung *Corvus* zurückzuführen sind.

Die Neukaledonienkrähen zeigten im Vergleich zu den drei anderen passeriformen Arten signifikant größere allometrische Indices für das Mesopallium, den striatopallidalen Komplex, das Septum und das Tegmentum. Die signifikante Vergrößerung ebendieser vier Hirnstrukturen ließ sich auch im Einzelvergleich mit den Rabenkrähen erkennen. Die Abbildungen 5 und 6 zeigen beispielhaft die Ergebnisse für das Mesopallium.

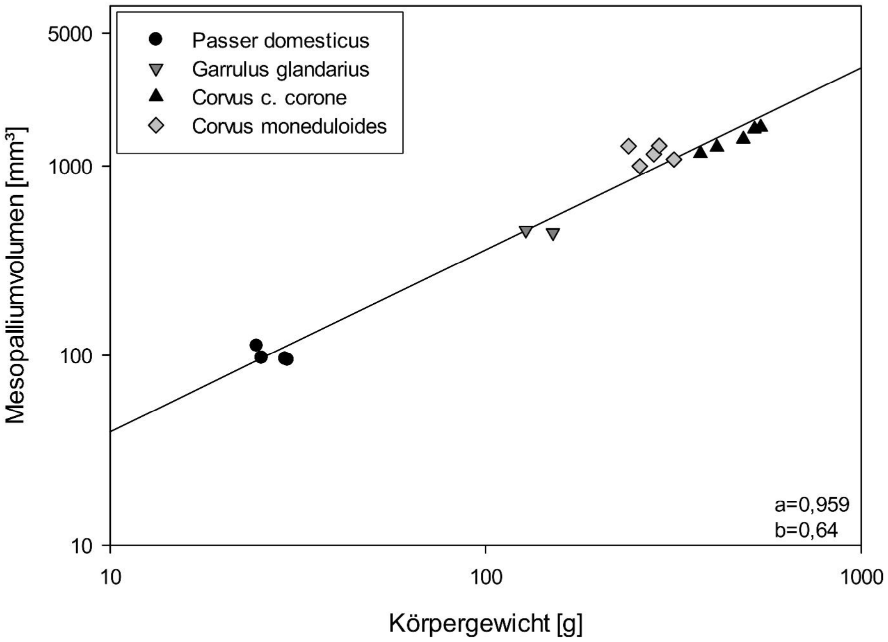


Abb. 5. Doppelt logarithmisch Auftragung des Mesopalliumvolumens vs. des Körpergewichtes von 16 Individuen aus vier Arten der Ordnung *Passeriformes.* Verwendung der Abbildung mit freundlicher Genehmigung des Karger Verlages (Mehlhorn et al., 2010).

Abb. 6. Vergleich der Indizes des Mesopalliums von 11 Individuen aus drei Arten der Ordnung *Passeriformes* (Haussperling, Eichelhäher, Rabenkrähe) und 5 Neukaledonienkrähen. Einzeldaten mit Mittelwert und Standardabweichung, rechts jeweils der Fehlerbalken, **p=0.002. Verwendung der Abbildung mit freundlicher Genehmigung des Karger Verlages (Mehlhorn et al., 2010).

Die Tatsache, dass vier Hirnareale der Neukaledonienkrähen im Vergleich zu den anderen passeriformen Arten vergrößert sind, bestätigt unsere Hypothese, wonach die beeindruckenden Fähigkeiten der Neukaledonienkrähe bezüglich Werkzeugherstellung und –gebrauch und Problemlösungsstrategien mit Vergrößerungen von Vorderhirnstrukturen einher gehen. Vor allem die relative Vergrößerung des Mesopalliums bestätigt vorangegangene Studien, die besagen, dass die Größe des Mesopalliums Hinweise auf innovatives und flexibles Verhalten bei Vögeln gibt [Timmermanns et al., 2000; Lefebvre et al., 2002]. Das Mesopallium ist ein rein assoziatives Hirnareal, d.h. es bekommt keinerlei direkte Afferenzen sensorischer Art. Sein ventraler Teil beinhaltet Areale, die für das Vokalisationslernen bei Singvögeln, Papageien und Kolibiris wichtig sind [Jarvis und Mello, 2000]. Der anteroventrale Teil, teilweise überlappend mit dem vorhergehenden, beinhaltet wichtige Areale für schnelles assoziatives Lernen im Kontext von Prägung und Vermeidungslernen [Rose, 2000; Horn, 2004]. Feenders et al. [2008] stellten sogar heraus, dass das Mesopallium Teil eines Regelkreises ist, der das Sequenzieren und Lernen von Bewegungen kontrolliert. Die Fähigkeiten des Werkzeuggebrauchs und der Werkzeugherstellung scheinen somit stark an das multimodale Vorderhirnareal in Form des Mesopalliums gekoppelt zu sein. Zu den besonderen Verhaltensweisen der Neukaledonienkrähen passt auch der relativ vergrößerte striatopallidale Komplex. Er ist äquivalent zum gleichnamigen Komplex im Säugerhirn und spielt neben seiner Einbindung in die Bewegungssteuerung auch eine Rolle bei diversen kognitiven Funktionen wie der Kategorisierung oder der Herstellung von Kontextbezügen [Ashby et al., 2007; Seger, 2008]. Kortikale und striatale Neurone bilden zudem Schaltkreise aus, die auf sensomotorische Lernvorgänge reagieren und sich währenddessen entsprechend verändern [Brasted und Wise, 2004]. Somit ist zu vermuten, dass die Vergrößerung dieses Bereiches in direktem Zusammenhang mit den kognitiven und motorischen Fähigkeiten der Neukaledonienkrähen steht, die ihnen zum einen ermöglichen, Werkzeug herzustellen, zum anderen aber auch der Anwendung diverser Werkzeuge auf verschiedene bekannte und unbekannte Situationen/Probleme dienen. Das Nidopallium der Neukaledonienkrähen ist zwar vergrößert, allerding erreicht dieser Unterschied keine Signifikanz. Warum aber nur das Mesopallium und nicht auch das Nidopallium signifikant vergrößert ist, darüber kann nur spekuliert werden. Es könnte damit zusammenhängen, dass das Nidopallium eher für kognitive und motorische Funktionen zuständig ist, die grundsätzlich für den Gebrauch von Werkzeugen wichtig sind. Das Mesopallium kommt vielleicht vor allem dann ins Spiel, wenn es um die Erweiterung und Verbesserung dieser Grundfähigkeiten geht. Die relativen Vergrößerungen des Septums und des Tegmentums sind durchaus interessant, aber aufgrund ihrer grundsätzlichen Funktionen scheinen sie in keinem direkten Zusammenhang zu den besonderen Fähigkeiten der Neukaledonienkrähen zu stehen.

Die Herstellung und der Gebrauch von Werkzeugen bei Neukaledonienkrähen ist nicht nur Teil eines starr ablaufenden motorischen Programmes, sondern rührt von kognitiven Fähigkeiten her, die flexibel auf Situationen reagieren können. Dies macht die Neukaledonienkrähe zum kompetentesten nicht-menschlichen Werkzeughersteller überhaupt. Die von uns nachgewiesenen Vergrößerungen der assoziativen Hirnareale könnten die neurale Basis dafür bilden. Zudem bestätigen unsere Ergebnisse die Theorie, dass die Evolution von Säuger- und Vogelgehirnen ähnlich verlief (Rehkämper und Zilles, 1991). Auch bei Primaten kann im Vergleich zu anderen Säugetieren eine relative Vergrößerung assoziativer Vorderhirnareale und des Striatum beobachtet werden [Stephan et al., 1988; Rehkämper et al., 1991a; Keverne et al., 1996; Barton und Harvey, 2000].

Erstmalig konnte mit den beiden vorangegangenen Studien ein Blick in die Neuroanatomie der Neukaledonienkrähe geworfen werden. Unsere Daten zeigen, dass die hohen kognitiven Fähigkeiten mit einer Volumenvergrößerung in entsprechenden assoziativen Vorderhirnarealen einhergehen. Oder, anders ausgedrückt, scheint die Vergrößerung assoziativer Vorderhirnareale eine notwendige Grundlage in der Evolution von kognitiven Fähigkeiten zu sein.

VI.2. Hirnbau und räumliche Kognition der Brieftaube (*Columba livia* f.d.)

VI.2.1. Volumetrische Untersuchungen

Im Zuge der Domestikation von Tieren wird in Bezug auf das Verhalten und auch Ausgestaltung des Gehirns häufig von einer „regressiven Evolution“ gesprochen, da viele Verhaltensweisen bei Haustieren nicht mehr oder nur noch rudimentär auftreten und auch die Hirngröße bei Haustieren im Vergleich zu ihren wilden Vorfahren reduziert zu sein scheint [Ebinger, 1980, 1995; Sossinka, 1982; Kruska, 1988, Herre und Röhrs, 1990; Hemmer, 1990]. Dabei beinhaltet der Begriff „regressiv“ durchaus eine negative Konnotation, die aber bei näherer Betrachtungsweise kritisch überdacht werden sollte (Rehkämper et al. 2001). Wenn die Evolution als ein Prozess angesehen wird, der mit gesteigerter Fitness einhergeht, die letztendlich zu einer höheren Anzahl an Nachkommen und einer weiteren Verbreitung führt, so wie es u.a. Haldane [1932], Thoday [1953], Maynard Smith [1982] und Gomulkiewicz [1998] postulieren, so müsste der Begriff „regressiv“ im Falle der Haustiere eigentlich das Gegenteil bedeuten. Schließlich ist es nicht zu leugnen, dass Haustiere ebenso weit verbreitet sind wie der Mensch (was den Lebensraum ihrer wilden Vorfahren weit übersteigt) und die Reproduktionsraten bei Haustieren enorm sein können und größtenteils nicht mehr mit denen der Vorfahren vergleichbar sind. Dies gilt im Prinzip für alle Haustiere, insbesondere aber für Geflügel, inklusive Tauben (domestizierte Tauben kommen weltweit vor, wohingegen die wilde Felsentaube lediglich im Mittelmeerraum verbreitet ist [Haag-Wackernagel, 1998]).

In einer ersten Untersuchung haben wir die Hypothese aufgestellt, dass Brieftauben hervorragend an die vom Menschen für sie generierte ökologische Nische angepasst sind und sich diese Anpassung auch in der Zusammensetzung des Gehirns wiederspiegelt [Rehkämper et al. 2008, **Publikation 3**]. Das Ziel war, zu überprüfen, ob es im Zuge der Domestikation nicht nur zu einer Reduktion der Hirn(teil)größe kommen kann, sondern auch als Reaktion auf die Selektion durch den Menschen auf bestimmte Eigenschaften hin, zu einer Größenzunahme bestimmter Strukturen. Vorangegangene Arbeiten deuteten gerade bei den Brieftauben bereits darauf hin [Rehkämper et al., 1988], allerdings in einem kleineren vergleichenden Rahmen. Zudem wurde kein direkter Bezug zum Wildtyp bzw. der wilden Stammform der Brieftaube hergestellt. In der vorliegenden Arbeit wurde ein allometrischer Vergleich angestellt (siehe auch V.1) und die Gehirne von Felsentauben (*Columba l. livia*), Brieftauben und vier weiteren Taubenrassen miteinander verglichen. Die Felsentauben gelten als wildlebende Stammform aller Haustauben und sind deshalb die referentielle Vergleichsform. Als Vergleichsrassen wurden Figurita Mövchen (aufgrund ihrer kleinen Größe), Orientalische Roller (aufgrund ihrer guten Flugeigenschaften), Sächsische Kröpfer (da sie sich phänotypisch sehr stark vom Wildtyp unterscheiden) und Kingtauben (aufgrund ihrer Größe und ihres schlechten Flugvermögens) ausgewählt. Ähnlich wie bei den Neukaledonienkrähen wurden Schnittserien von den Gehirnen angefertigt, diese versilbert und die Einzelkomponenten der Gehirne vermessen, i.e. der Hirnstamm, das Tectum opticum (inklusive Tractus opticus), das Diencephalon, das Cerebellum und das Telencephalon. Vom Telencephalon wurden zusätzlich sieben Einzelkomponenten separat ausgewertet: (1) Hyperpallium apicale+densocellulare, (2) Mesopallium, (3) Nidopallium (inklusive Entopallium und Arcopallium), (4) Striatum (Striatum laterale+Striatum mediale+Globus pallidus+Tuberculum olfactorium), (5) Hippocampus, (6) Septum und (7) Bulbus olfactorius (Abb. 7).

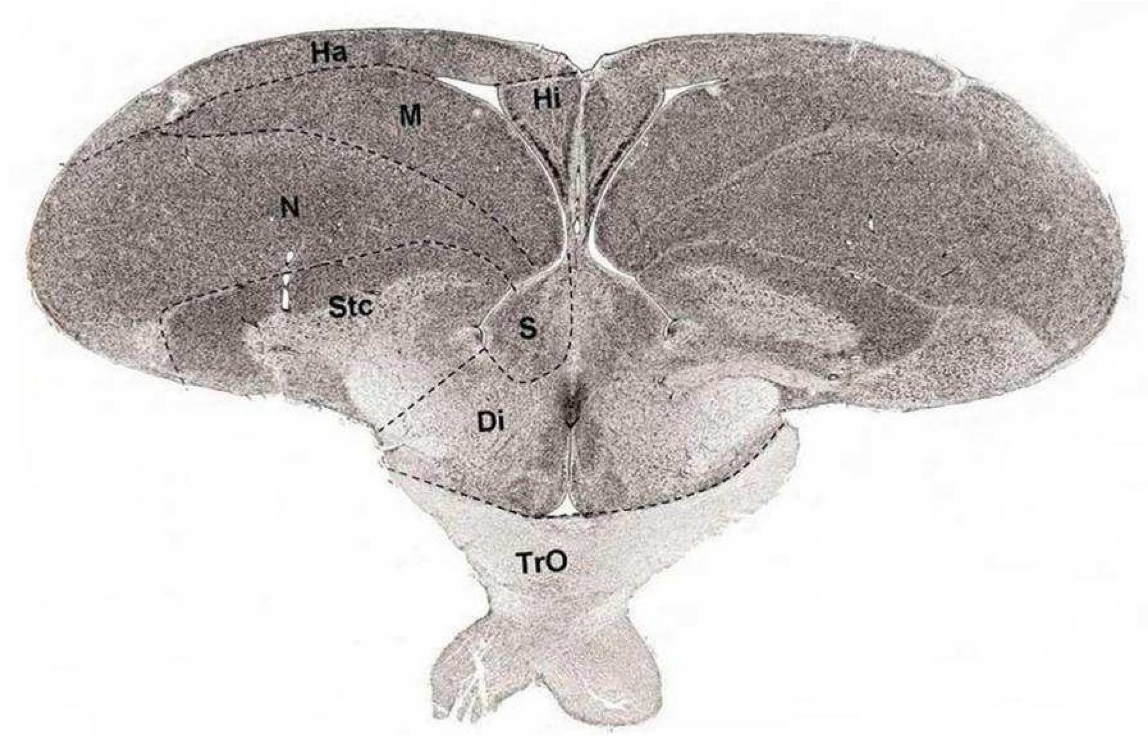


Abb. 7. Frontalschnitt durch das Gehirn einer Brieftaube zur Illustration einiger Hirnreale. Di=Diencephalon, Ha=Hyperpallium apicale, Hi=Hippocampus, M=Mesopallium, N=Nidopallium, Stc=Striatopallidaler Komplex, S=Septum, TrO=Tractus opticus. Versilberung nach Gallyas. Verwendung der Abbildung mit freundlicher Genehmigung des Karger Verlages (Rehkämper et al., 2008).

Im Vergleich zur Felsentaube zeigte sich, dass zwar im Prinzip bei allen Taubenrassen (inklusive den Brieftauben) das Nettohirnvolumen, das Volumen des Cerebellums und des Telencephalons im Ganzen signifikant kleiner war (Abb. 8), es aber auch mehrere Hirnstrukturen gab, wo kein Größenunterschied vorlag. Dies galt vor allem für als konservativ geltende Hirnteile wie das Tegmentum. Interessanterweise gab es bei allen Rassen auch einzelne Strukturen, die im Vergleich zur Felsentaube signifikant größer waren. So ist das Telencephalon im Ganzen zwar kleiner bei den Rassetauben, der Hippocampus folgt diesem Trend jedoch nicht und ist bei allen Rassen signifikant größer im Vergleich zur Wildform (Abb. 9). Dabei stachen vor allem die Rassen mit guten Flugfähigkeiten wie die Figurita Mövchen, die Orientalischen Roller und die Brieftauben hervor. Sowohl bei Mövchentauben als auch bei Rollertauben wird vermutet, dass sie zu Beginn der Zucht der modernen Brieftaube einen großen Einfluss auf die Zucht hatten [Levi, 1965]. Untersucht man die Position der Brieftaube innerhalb der untersuchten Taubenrassen, so fällt auf, dass auch hier ein signifikant größerer Hippocampus vorliegt und zudem auch noch der Bulbus olfactorius im Vergleich zu den anderen Rassen signifikant vergrößert ist.

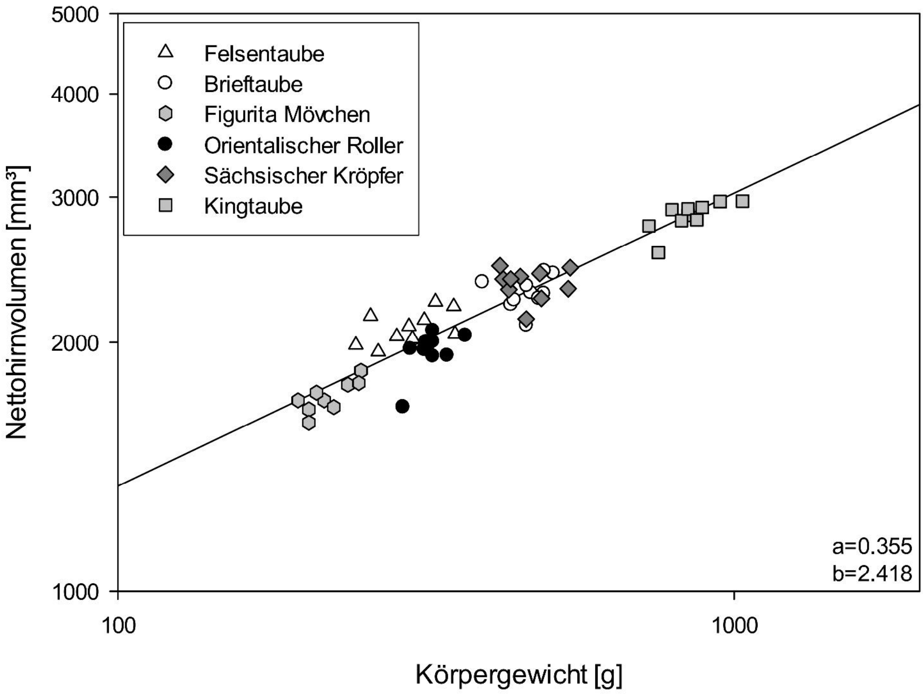


Abb. 8. Nettohirnvolumen (mm³) von Felsentauben und fünf Haustaubenrassen inklusive der Brieftaube in Relation zum Körpergewicht. Verwendung der Abbildung mit freundlicher Genehmigung des Karger Verlages (Rehkämper et al., 2008).

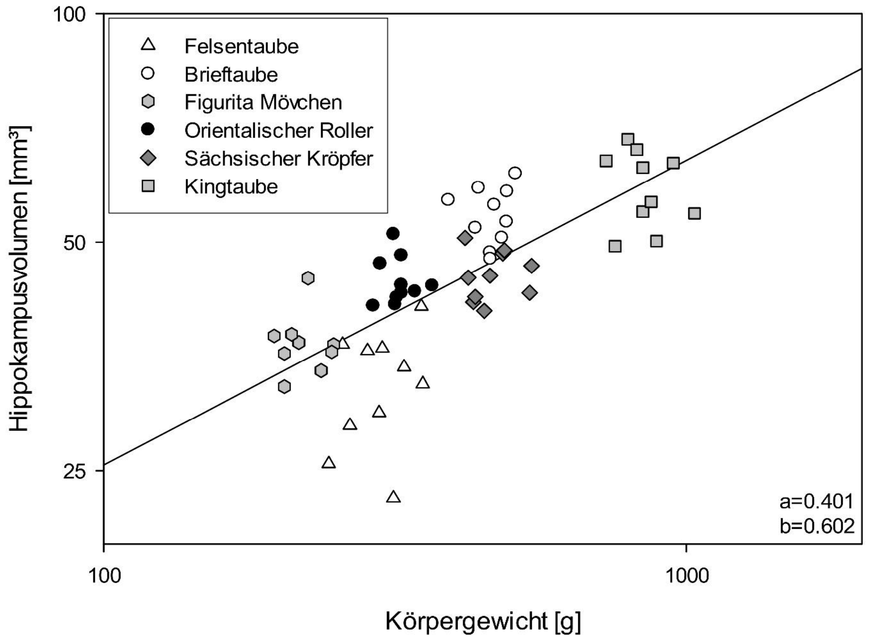


Abb. 9. Hippocampusvolumen (mm³) von Felsentauben und fünf Haustaubenrassen inklusive der Brieftaube in Relation zum Körpergewicht. Verwendung der Abbildung mit freundlicher Genehmigung des Karger Verlages (Rehkämper et al., 2008).

Diese Ergebnisse stehen im Gegensatz zu der Hypothese einer „regressiven Evolution“ als Folge der Domestikation. Die hier erzielten Ergebnisse konnten zeigen, dass die Selektion des Menschen und die Anpassung des domestizierten Tieres an die ökologische Nische „Mensch“ durchaus auch zur Vergrößerung von Hirnteilen führen kann. Der Hippocampus ist hier die erste dokumentierte Struktur, bei der es erwiesenermaßen unter den Bedingungen der Domestikation zu einer Größenzunahme im Vergleich zur Wildform gekommen ist. Die Tatsache, dass Brieftauben auch im Vergleich zu anderen Taubenrassen noch einmal durch ihren vergrößerten Hippocampus und einen vergrößerten Bulbus olfactorius herausstechen, bestätigt die Ergebnisse von Rehkämper et al. [1988] und spricht für eine funktionelle Anpassung an das „Heimfinden“, was in dieser extremen Form nur bei Brieftauben vorliegt und auf räumlicher Kognition und der Integration von sensorischen (u.a. olfaktorischen) Informationen basiert.

VI.2.2. Nature vs. Nurture. Der Einfluss von Erfahrung auf den Hirnbau

Auf neuronaler Ebene spielt, sowohl bei Säugetieren als auch bei Vögeln, erwiesenermaßen der Hippocampus eine Schlüsselrolle bei der Verarbeitung räumlicher Informationen [Rehkämper, 1981; Stephan et al., 1991; Bingman, 1993; Atoji et al., 2002; Jacobs, 2003; Nadel und Hardt, 2004]. Bingman [2003] konnte sogar zeigen, dass das Heimfindevermögen von Brieftauben maßgeblich mit der Hippocampusfunktion zusammenhängt. Die vorhergehende Studie [Rehkämper et al., 2008] hat bereits dargelegt, dass das Gehirn der Brieftaube funktionell auf ein sehr gutes Heimfindevermögen angepasst ist und dass der Hippocampus dabei eine hohe Relevanz hat. In einer zweiten Untersuchung haben wir überprüft, ob solch eine Anpassung nicht nur zu einer Vergrößerung bestimmter Hirnstrukturen im Allgemeinen führt, sondern auch individuell im Laufe der Ontogenese durch Erfahrung hervorgerufen werden kann [Cnotka et al., 2008 **Publikation 4**]. Bis dahin konnte dies lediglich bei futterversteckenden Vögeln und Zugvögeln gezeigt werden, deren Hippocampusgröße mit dem Maß an individueller Erfahrung korreliert [Clayton und Krebs, 1994; Clayton, 1996; Healy et al., 1996]. In der vorliegenden Arbeit wurden die Gehirne von Brieftauben aus der eigenen Zucht miteinander verglichen, die zwar zusammen aufgewachsen waren, aber nach Erreichen der Flugfähigkeit in zwei Gruppen eingeteilt wurden. Die erste Gruppe verblieb zeitlebens im Schlag, dessen Größe es allerdings ermöglichte, dass auch diese Tiere es lernen konnten zu fliegen. Die andere Gruppe hatte täglich Gelegenheit zum Freiflug und nahm zudem an mehreren organisierten Wettflügen von bis zu 250 km Länge teil. Tiere der zweiten Gruppe konnten also viel Navigationserfahrung sammeln. Nach Beendigung des ersten Lebensjahres wurden (wie bei den vorangegangenen Studien) den Tieren beider Gruppen die Gehirne entnommen, aufgearbeitet und volumetrisch vermessen. Das Volumen des Gesamthirns, des Telencephalons, des Hippocampus und von 12 weiteren Hirnstrukturen wurde unter Zuhilfenahme eines Allgemeinen Linearen Modells miteinander verglichen. Es zeigte sich, dass die Tiere mit Navigationserfahrung einen in Relation zum Telencephalon 11,2 % größeren Hippocampus aufwiesen als die Tiere ohne Navigationserfahrung (Abb. 10). Dies ist konsistent mit vorangegangenen verhaltensbiologischen Studien, die eine verminderte Navigations- und Orientierungsfähigkeit bei Tieren zeigten, die nur im Schlag gehalten wurden [Bingman and Mench, 1990; Gagliardo et al., 2007]. Die vorliegende Arbeit konnte erstmalig zeigen, dass es beim Heimfindevermögen der Brieftaube neben der unbestrittenen genetischen Komponente auch eine Komponente gibt, die durch Erfahrung beeinflusst wird. Die individuelle Lebensgeschichte ("life history") hat also augenscheinlich einen größeren Einfluss auf den Hirnbau bzw. Hirnteilgrößen als bisher angenommen. Erfahrung ist offenbar eine Vorbedingung dafür, dass das Entwicklungspotential des Hippocampus voll ausgeschöpft werden kann.

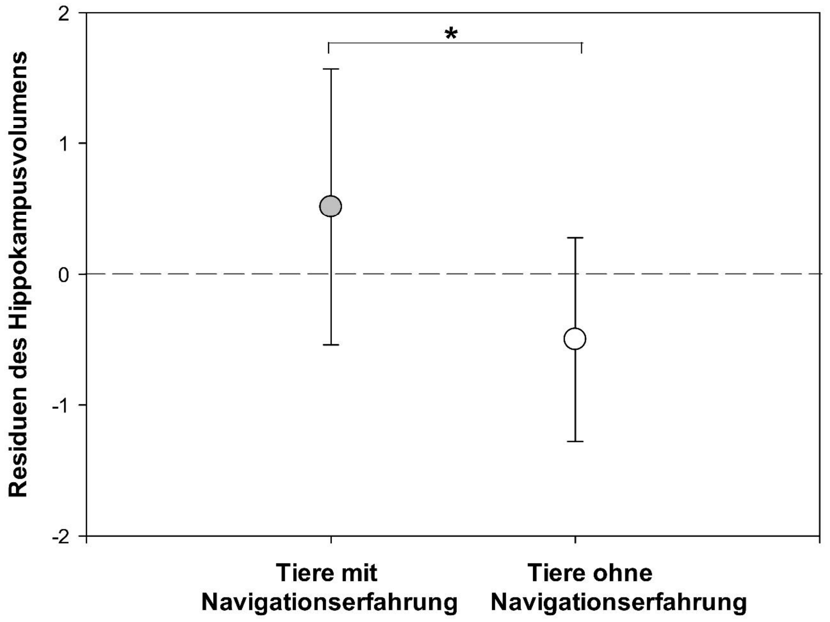


Abb. 10. Auf dem Allgemeinen Linearen Modell basierende Residuen des Hippocampusvolumens in Relation zum Telencephalon von Brieftauben mit und ohne Navigationserfahrung, *p=0.028. Verwendung der Abbildung mit freundlicher Genehmigung des Karger Verlages (Cnotka et al., 2008a).

Somit leisten die beiden vorangegangen Untersuchungen [Cnotka et al., 2008; Rehkämper et al., 2008] auch einen Beitrag zur so genannten „Nature vs. Nurture“-Debatte (oder auch „Anlage-Umwelt-Problem) und unterstützen dabei sowohl Burrhus Frederic Skinner, der als Befürworter der Umwelt-Theorie davon ausging, dass jegliches Verhalten und jegliche Fähigkeit abhängig von individuellen Erfahrungswerten ist und konditioniert werden könne, als auch Charles Darwin, der eher eine Anlagen-Theorie vertrat, wonach sämtliche Verhaltensweisen und Fähigkeiten erblich bedingt sind [Sherry et al., 2004; Vincent und Brown, 2005].

Funktionelle Spezialisierungen der rechten und linken Hirnhälfte („Lateralisation“) lassen sich auch bei Vögeln beobachten und sind bei Tauben unter anderem bereits für die Verarbeitung visueller Reize oder auch Aspekte des räumlichen Lernens und des räumlichen Gedächtnisses dokumentiert [z.B. Rogers, 1996; Güntürkün, 1997a; Ulrich et al., 1999; Gagliardo 2001; Kahn und Bingman, 2004]. Morphologische Spezialisierungen oder Asymmetrien sind weitaus seltener untersucht worden und bisher hauptsächlich für das Tectum opticum beschrieben, wo unterschiedliche Zellgrößen in den verschiedenen Schichten vorliegen [Güntürkün, 1997a], sowie für den rechten und linken Hippocampus, bei dem jeweils verschiedenartige Zelltypen nachgewiesen wurden [Hough und Bingman, 2004; Siegel et al., 2006]. Durch unsere beiden vorhergehenden Arbeiten [Cnotka et al., 2008; Rehkämper et al., 2008] konnte bereits gezeigt werden, dass das Brieftaubengehirn (1) morphologisch an das Merkmal „Heimfinden“ angepasst ist und (2) plastisch auf (Navigations-) Erfahrung reagiert. Der Umstand, dass es auch (zumindest funktionell) lateralisiert ist, führte nun zu der Frage, in welcher Art und Weise sich Lateralisation im Hirnstrukturvolumen widerspiegelt und ob mögliche Asymmetrien durch individuelle Erfahrungen verursacht oder zumindest beeinflusst werden.

Dieser Frage wurde in der nachfolgenden Arbeit nachgegangen [Mehlhorn et al., 2010; **Publikation 5**]. Methodisch wurden hierfür ebenfalls die Gehirne von Brieftauben mit viel Navigationserfahrung und Brieftauben ohne Navigationserfahrung untersucht und miteinander verglichen. Acht telencephale Hirnstrukturen (Hyperpallium apicale, Hyperpallium densocellulare, Mesopallium, Nidopallium (inklusive Arcopallium und Entopallium), der striatopallidale Komplex (mit Globus pallidus, Striatum laterale und mediale und Tuberculum olfactorium), Hippocampus, Septum und Bulbus olfactorius wurden separat für die rechte und linke Hemisphäre vermessen. Zusätzlich wurde das Volumen von Cerebellum, Diencephalon, Tectum opticum, Tractus opticus, Tegmentum und Telencephalon im Ganzen bestimmt, um ein Nettohirnvolumen errechnen zu können. Aufgrund der beschriebenen morphologischen Asymmetrien und seiner Rolle bei der Verarbeitung visueller Informationen [Güntürkün, 1997a] wurde das rechte und linke Tectum opticum ebenfalls separat vermessen. Vogelmodelle eignen sich durch ein nahezu vollständiges Überkreuzen der Sehnerven und das weitgehende Fehlen eines Corpus callosum oder anderer funktionell entsprechender Strukturen gut für die Erforschung von Hemisphärenunterschieden. Der visuelle Input eines Auges wird überwiegend in der gegenüberliegenden Hirnhälfte verarbeitet.

Es zeigte sich, dass Tiere mit Navigationserfahrung ein stärker lateralisiertes Gehirn aufweisen als Tiere ohne Navigationserfahrung, so dass es hier mehr Rechts/Links-Unterschiede gibt. Im Detail bedeutet dies, dass bei Tieren mit Navigationserfahrung ein größeres(r) linkes Hyperpallium apicale, rechtes Nidopallium, linker Hippocampus und rechtes Tectum opticum vorliegen. Tiere ohne Navigationserfahrung zeigen lediglich ein größeres linkes Hyperpallium apicale (Abb. 11).

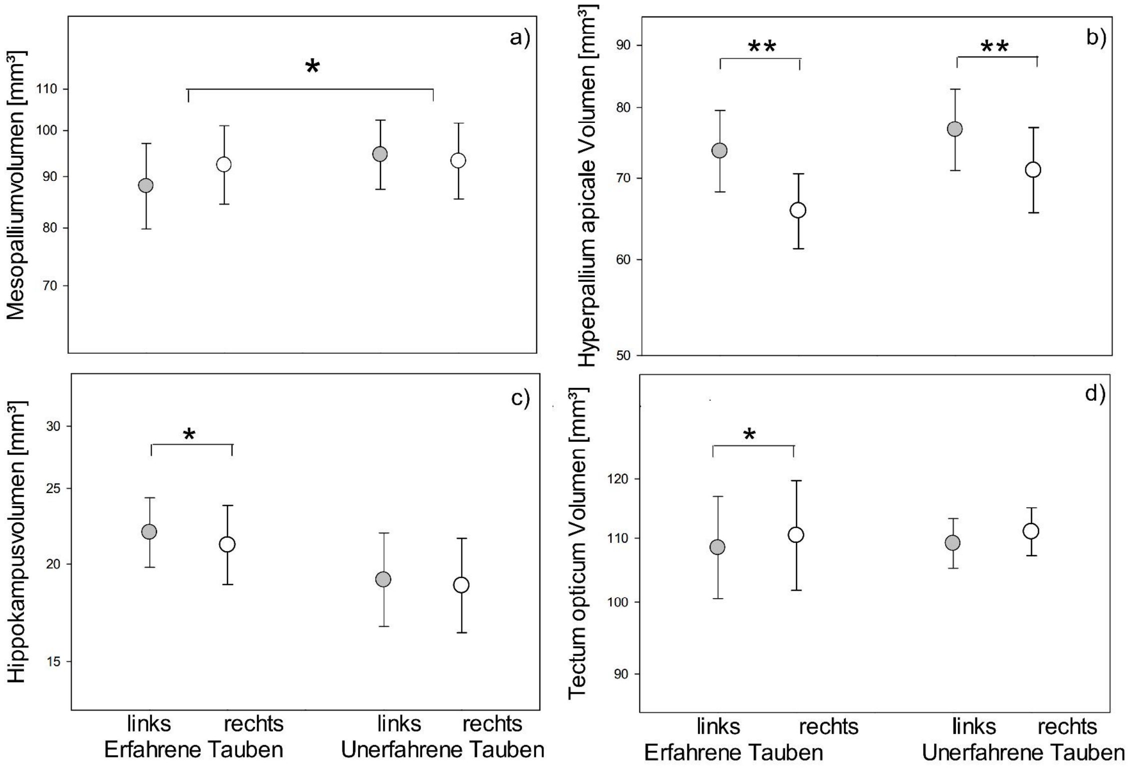


Abb. 10. Rechtes und linkes Volumen diverser Hirnstrukturen von Brieftauben mit und ohne Navigationserfahrung. Dargestellt sind die geometrischen Mittelwerte mit 95% Konfidenzintervallen, * $p<0.05$, **$p<0{,}01$. Verwendung der Abbildung mit freundlicher Genehmigung von Journal of Experimental Biology (Mehlhorn et al., 2010b).

Der Befund des vergrößerten linken Hyperpallium apicale in beiden Gruppen ist hierbei insofern interessant, dass er zwar nicht einen Einfluss von Erfahrung wiederspiegelt, jedoch erstmalig eine (volumetrische) Lateralisation im thalamofugalen System von Vögeln dokumentiert. Das Hyperpallium apicale ist als Teil des so genannten „Wulstes“ (bestehend aus Hyperpallium apicale, densocellulare und intercalatum) mit für die Verarbeitung visueller Informationen für die Orientierung zuständig und bekommt seine (visuellen) Informationen (im Unterschied zum tectofugalen System mit dem Tectum opticum als Hauptkomponente) aus dem dorsalen Thalamus [Güntürkün, 1991; Shimizu und Bowers, 1999]. Somit scheint es hier eine weitere Anpassung des Gehirns an das Heimfinden zu geben, die allerdings unempfindlich auf Erfahrung reagiert und bei der das betreffende Hirnareal nicht generell vergrößert ist. Die anderen beobachteten Asymmetrien, in erster Linie die Vergrößerung des linken Hippocampus bei navigationserfahrenen Tieren, können wieder als art- bzw. verhaltensspezifische Anpassung auf das Heimfinden bzw. die Navigation hin interpretiert werden. Die oben aufgeführten Ergebnisse entstammen alle aus Vergleichen innerhalb der beiden Gruppen. Der Vergleich von Rechts-Links-Quotienten zwischen beiden Gruppen zeigte zusätzlich noch, dass Tiere mit Navigationserfahrung ein kleineres linkes Mesopallium im Vergleich zum rechten Mesopallium aufweisen, während Tiere ohne Navigationserfahrung ein im Vergleich zum linken Mesopallium kleineres rechtes Mesopallium aufweisen (Abb. 10 a). Dies ist umso erstaunlicher, als bei Vögeln generell der rechten Hemisphäre zugeschrieben wird vor allem an der Vermittlung von emotionalen und instinktgeleiteten Reaktionen beteiligt zu sein. Der linken Hemisphäre wird zugeschrieben, dass sie sich vornehmlich mit erfahrungsabhängigen Verhaltensweisen befasst [MacNeilage et al., 2009; Valencia-Alfonso et al., 2009]. Da das Mesopallium zudem in der Regel mit kognitivem Verhalten assoziiert wird [Lefebvre et al., 2004], und Navigieren als eine kognitive Leistung anzusehen ist, wäre eher bei den Tieren mit Navigationserfahrung eine größeres linkes Mesopallium zu erwarten gewesen. Zumal es keinen absoluten Volumenunterschied zwischen dem linken Mesopallium der Tiere beider Gruppen gab. Hier wären weitere Untersuchungen zur Rolle des Mesopalliums beim Navigieren interessant und aufschlussreich.

Abschließend kann gesagt werden, dass die vorgefundenen volumetrischen Lateralisationen als eine Anpassung auf das Heimfinde- bzw. Navigationsverhalten angesehen werden können und wahrscheinlich der besseren Effizienz in der Verarbeitung von Informationen dienen. Zudem bestätigen sie die so genannte „Mosaik-Theorie“, nach der die Expansion spezifischer Hirnareale unabhängig von anderen Arealen erfolgen kann [Barton und Harvey, 2000; Rehkämper et al. 2008]. Das Gehirn der Brieftaube ist somit ein Beispiel für eine Mosaikevolution oder modulare Evolution unter den Bedingungen der Domestikation. Neben Umweltfaktoren wie Lichteinfall, Körperhaltung, sozialen Faktoren bei der Aufzucht oder Testosterongabe [Andrew et al., 2009; Pfannkuche et al., 2009; Schaafsma et al., 2009] konnte ein weiterer einflussnehmender Faktor auf die Lateralisation des Gehirns, nämlich die Erfahrung, dokumentiert werden, der sich in einer volumetrisch nachweisbaren Asymmetrie äußert.

VI.2.3. Der Einfluss von Erfahrung auf die räumliche Kognition

Da die vorhergehenden Arbeiten zeigen konnten, dass Tiere mit Navigationserfahrung einen größeren Hippocampus und ein stärker lateralisiertes Gehirn aufweisen als Tiere ohne Navigationserfahrung, wurde als nächstes der Frage nachgegangen, inwiefern Erfahrung einen Einfluss auf die Navigations- oder Orientierungsfähigkeit hat. Dazu wurden Verhaltensuntersuchungen in einer zweidimensionalen Umgebung, hier in einer so genannten Skinner-Box mit einem Touchscreen-Monitor durchgeführt. Diese stellt ein reizarmes Behältnis dar, in dem Experimentaltiere standardisiert und überwiegend automatisiert neue Verhaltensweisen erlernen können. Die Funktionsweise der Skinner-Box basiert auf dem Prinzip der operanten Konditionierung, d.h. der Einflussnahme auf die Verhaltensweise eines Tieres mittels Belohnung für erwünschtes Verhalten und ausbleibender Belohnung bzw. Bestrafung für unerwünschtes Verhalten.

Mehrere Studien konnten bereits zeigen, dass für die Orientierung in vertrauter Umgebung bzw. in der Nähe des heimatlichen Schlages (<5km) vor allem visuelle Landmarken eine wichtige Rolle spielen [Wallraff, 2005; Cheng et al., 2006; Wiltschko et al., 2007]. Zusätzlich können geometrische Informationen wie die Oberflächenbeschaffenheit oder -proportionen als Informationsquelle dienen, wobei bis heute noch nicht klar ist, wann welche dieser Informationen in welchem Ausmaß genutzt werden [Kelly et al., 1998; Tommasi et al., 2012]. Kelly & Spetch konnten 2004 zeigen, dass eine Skinner-Box mit eingebautem Touchscreen zur experimentellen Überprüfung der Orientierungsfähigkeit auf zweidimensionaler Ebene bzw. der Nutzung von geometrischen Informationen bzw. Landmarken dienen kann. Die Tiere wurden mittels operanter Konditionierung darauf trainiert, auf bestimmte Bereiche eines Stimulus zu picken. Dieser Stimulus umfasste sowohl geometrische Informationen (in Form von einem Rechteck), als auch verschiedenfarbige Symbole (als Landmarken). Hierbei konnte bereits gezeigt werden, dass die Tiere sowohl die Proportionen des Rechtecks zum Auffinden des belohnten Zielbereichs nutzen konnten als auch die Symbole, die hier im Experiment als visuelle Landmarken dienten.

Im Fokus unserer Arbeit [Mehlhorn und Rehkämper, 2017, **Publikation 6**] stand wieder eine innerartliche Gegenüberstellung zweier Gruppen von Brieftauben mit unterschiedlicher Navigationserfahrung. Es wurde hierbei ein an Kelly und Spetch [2004] angelehntes experimentelles Design genutzt. Die Abb. 11 zeigt den auf dem Touchscreen-Monitor sichtbaren Stimulus. Die Tiere wurden über verschiedene Phasen und mittels eines Vortrainings gefolgt von einem Training darauf konditioniert, auf ein individuell und randomisiert zugeordnetes, weißes Antwortfeld zu picken, welches mit einer bestimmten Ecke bzw. geometrischen Information (z.B. kurze Seitenlinie rechts, lange Seitenlinie links) und einer Landmarkeninformation (Symbole, z.B. rotes Dreieck) assoziiert war.

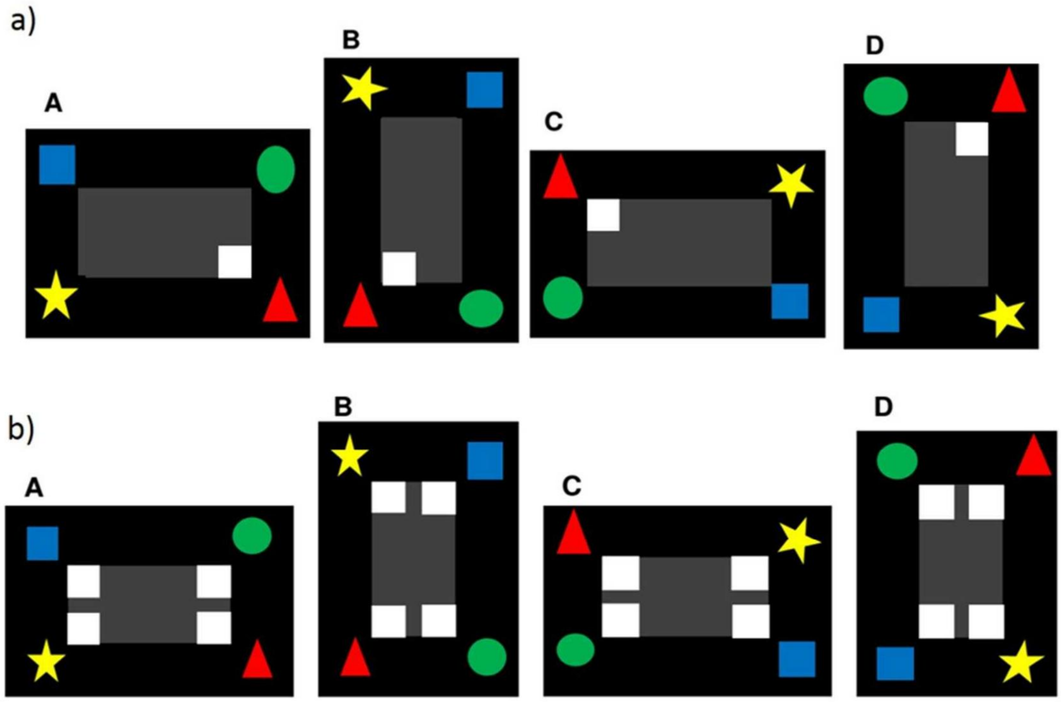


Abb.11. Anzeige des Touchscreen-Monitors während des Vortrainings (a) und des Trainings (b) mit jeweils einem oder vier identischen weißen Antwortfeldern. In diesem Beispiel wurde auf das rote

Dreieck in der Ecke mit der langen Seite links und der kurzen Seite rechts konditioniert. Der Stimulus rotierte während einer Experimentalsitzung (A: 0°; B: 90°; C: 180°; D: 270°). Die Bildrechte liegen bei der Autorin (Quelle: Mehlhorn und Rehkämper, 2017).

Nach erfolgreichem Training wurde der Stimulus für mehrere Tests modifiziert (Abb.12):

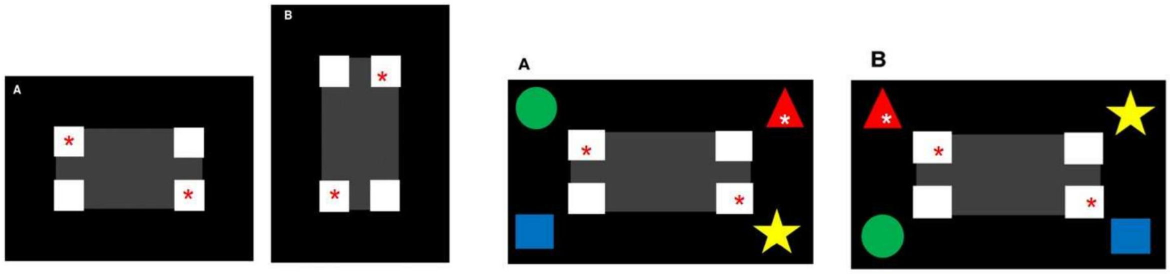
a) Im **Geometrietest** wurden alle Symbole/Landmarken entfernt, so dass nur noch die geometrische Information des grauen Rechtecks verfügbar war, um die belohnte Ecke aufzufinden.

b) Im **Affinitätstest** rotierten die Symbole/Landmarken im Uhrzeigersinn um das Rechteck, so dass es zu einer Diskrepanz zwischen der korrekten geometrischen Information und der korrekten Landmarke kommen konnte. Die Taube musste sich entscheiden, welche Art von Information sie für wichtiger hält, um sich für ein Antwortfeld zu entscheiden.

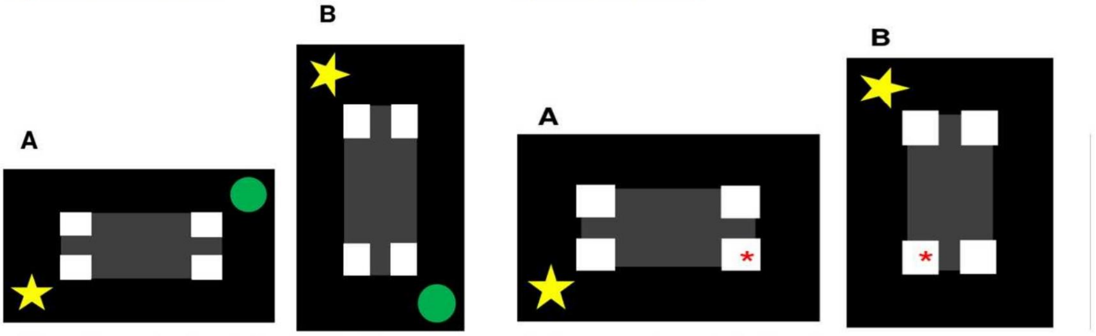
c) Im **Landmarkentest (nah & fern)** wurden das Symbol/die Landmarke der belohnten Ecke und der diagonalen Ecke entfernt, so dass nur noch die Symbole der Ecken mit der falschen geometrischen Information sichtbar waren.

d) Im **Landmarkentest (fern)** wurde ein weiteres Symbol entfernt, so dass nur noch das Symbol am Ende der langen Seite des Rechtecks (mit einer falschen geometrischen Information) gezeigt wurde.

Beide Landmarkentests dienten der Überprüfung, ob Tauben auch Symbole bzw. Landmarken nutzen können, auf die sie nicht direkt konditioniert wurden und ob sie sich auch Informationen über die relative Lage der anderen Landmarken in Bezug auf die belohnte Ecke einprägen.



a) Geometrietest b) Affinitätstest



c) Landmarkentest (nah&fern) d) Landmarkentest (fern)

Abb. 12. Beispiele für die Teststimuli. Zum besseren Verständnis markieren hier der rote (bzw. weiße) Stern die belohnte Ecke bzw. Landmarke (hier das rote Dreieck mit der langen Seite links und der kurzen Seite rechts). Auch hier rotierte der Stimulus wieder im Uhrzeigersinn; gezeigt werden die 0° (A) und 90° (B) Ausrichtung. Die Bildrechte liegen bei der Autorin (Quelle: Mehlhorn und Rehkämper, 2017).

Aufgrund der Tatsache, dass bei Tauben visuelle Informationen eines Auges im Chiasma opticum nahezu komplett auf die kontralaterale Seite kreuzen und somit primär erst einmal in der kontralateralen Hirnhälfte verarbeitet werden, lassen sich durch Abdeckung jeweils eines Auges Rückschlüsse auf die weitere Verarbeitung ziehen. Somit wurden alle Tests sowohl unter binokularen, als auch monokularen Sichtbedingungen durchgeführt.

Den Tieren beider Gruppen gelang es in allen Tests, sich anhand von geometrischen Informationen und Landmarken zu orientieren, wobei der Affinitätstest zeigte, dass die Verwendung von Landmarken gegenüber der Verwendung von geometrischen Informationen deutlich bevorzugt wurde. Tiere mit Navigationserfahrung zeigten zwar keine statistisch nachweisbar besseren Testergebnisse, die Verknüpfung beider Informationsarten war allerdings besser. Zudem gelang bei Ihnen die Konditionierung auf den Stimulus besser und schneller. Tiere ohne Navigationserfahrung benötigten für das Vortraining und Training signifikant mehr Zeit. Im Geometrietest schnitten die Tiere mit

Navigationserfahrung zwar besser ab, allerdings ließ sich dieser Unterschied nicht statistisch nachweisen (Abb. 13). Die Erfolgsrate war hier unabhängig davon, ob der Test mit beiden Augen oder nur mit dem rechten oder linken Auge durchgeführt wurde. Das spricht dafür, dass die Verarbeitung geometrischer Informationen in beiden Hirnhemisphären stattfindet und deckt sich mit der Studie von Wilzeck et al., 2009, die zeigte, dass zwar in der linken Hemisphäre vor allem absolute Distanzen entschlüsselt werden und in der rechten Hemisphäre relationale geometrische Informationen, es sich bei beiden jedoch um geometrische Informationen handelt. Ähnlich sieht es beim Affinitätstest aus, der sehr deutlich machte, dass Landmarken bevorzugt werden (Abb. 14). Auch hier fehlen Rechts-/Links-Unterschiede, was dafür spricht, dass beide Hemisphären Informationen aus Landmarken mehr gewichten bzw. ihnen eine größere Relevanz zukommt als geometrischen Informationen.

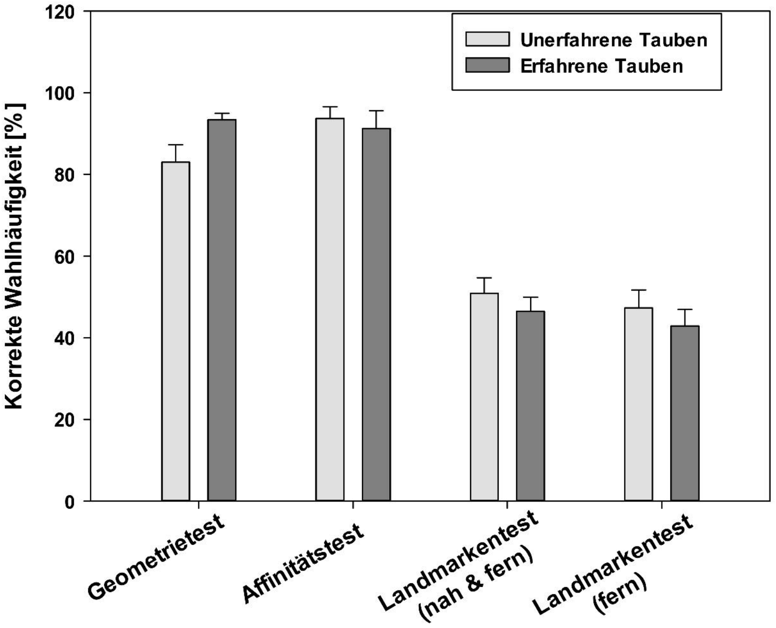


Abb. 13. Wahlhäufigkeiten der korrekten Ecke (Affinitätstest: Wahl des korrekten Symbols) über beide Taubengruppen in allen Tests (mit binokularer Sicht) gemittelt. Balken mit Standardfehler dargestellt. Die Bildrechte liegen bei der Autorin (Quelle: Mehlhorn und Rehkämper, 2017).

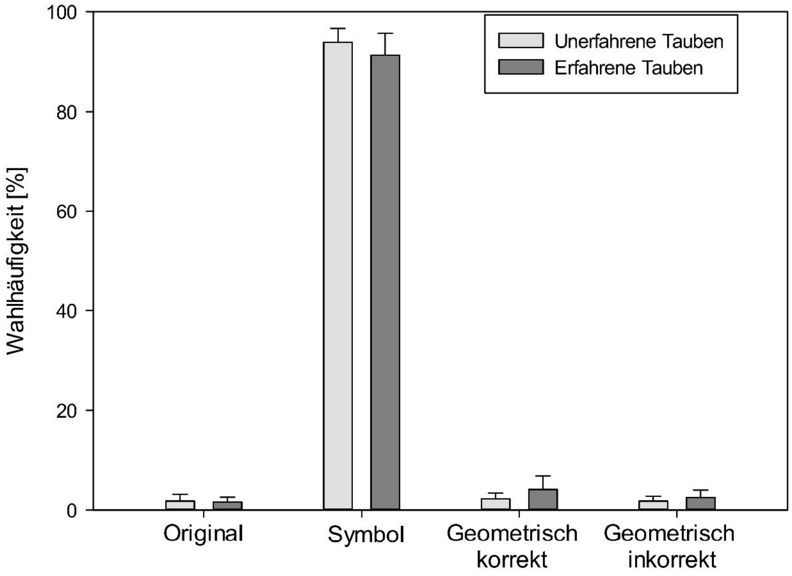


Abb. 14. Wahlhäufigkeiten der verschiedenen Ecken im Affinitätstest von beiden Taubengruppen (mit binokularer Sicht). Balken mit Standardfehler dargestellt. Die Bildrechte liegen bei der Autorin (Quelle: Mehlhorn und Rehkämper, 2017).

In den beiden Landmarkentests ergaben sich etwas komplexere Ergebnisse. Generell demonstrierten beide Gruppen, dass sie auch anhand von nur einer oder zwei weiter von der belohnten Ecke entfernten Landmarke(n) das richtige Antwortfeld lokalisieren konnten. Die Erfolgsrate war allerdings sehr viel schlechter als bei den anderen Tests (Abb. 13). Den Tieren fiel es schwerer, die Ecken voneinander zu unterscheiden, was natürlich Auswirkungen auf die Wahlhäufigkeit der korrekten Ecke hatte. Vor allem bei den Tieren ohne Navigationserfahrung konnten zudem noch signifikante Unterschiede zwischen dem Absolvieren der Tests mit beiden Augen und nur einem Auge festgestellt werden. Die Differenzierung zwischen den unterschiedlichen Ecken war bei ihnen signifikant schlechter, wenn sie die Tests nur mit dem rechten oder linken Auge absolvieren mussten. Dabei konnten keine Unterschiede zwischen den Augen festgestellt werden. Allem Anschein nach fällt es diesen Tieren entweder schwerer, geometrische Informationen und Landmarken gleichzeitig zu nutzen oder die Verknüpfung von mehreren Landmarken ist für ihre Orientierungsleistung wichtiger.

Die hier erzielten Ergebnisse deuten somit darauf hin, dass die individuelle Erfahrung oder das Ausmaß, in dem die Tiere verschiedenen Umweltreizen ausgesetzt sind, einen positiven Einfluss auf die Fähigkeit haben, verschiedene Merkmale für die Orientierung miteinander zu verknüpfen. Oder, vice versa, je weniger (Landmarken-) Informationen vorhanden sind, desto wichtiger wird die Vorerfahrung der Tiere. In unserer Studie konnte keine Dominanz einer Hemisphäre erkannt werden. Die heterogenen Ergebnisse bezüglich der Landmarkentests unter monokularen Sichtbedingen zeigten jedoch, dass es durchaus Unterschiede zu geben scheint. Die Organisation der Verarbeitung räumlicher Information scheint aber offenbar um einiges vielschichtiger und komplexer zu sein als bisher angenommen. Anscheinend findet die Verknüpfung von geometrischen Informationen und Landmarkeninformationen erst statt, nachdem sie separat in den beiden Hemisphären verarbeitet wurden. Dieser Prozess scheint durch Erfahrung beeinflussbar. Aufgrund der Parallelen zu Befunden beim Menschen könnte dies auf eine gemeinsame Grundlage der Lateralisationsentwicklung bei Wirbeltieren hindeuten [Wilzeck et al., 2009]. Insgesamt zeigen die erlangten Ergebnisse hinsichtlich mehrerer wichtiger Fragen der Lateralisationsforschung, wie die Erfahrungsabhängigkeit oder die Interaktion der Hemisphären, dass die bisherigen Ansichten über die Verarbeitung von Raum- und Objektinformation bei Vögeln einer kritischen Überarbeitung bedürfen.

VI.2.4. Der Einfluss von sozialen Parametern auf das Navigationsvermögen

Die vorangegangene Arbeit hat sich thematisch mit dem Orientierungsverhalten im zweidimensionalen Raum befasst und dort experimentell den Einfluss von Erfahrung auf die Orientierungsleistung untersucht. Ebenfalls interessant (und durchaus praxisbezogener) sind Untersuchungen zur Orientierungsleistung im dreidimensionalen Raum, d.h. auf tatsächlich geflogenen Strecken von bekannten oder unbekannten Auflassorten. In den vergangenen Jahren wurde eine Vielzahl von Untersuchungen publiziert, in denen es um das Heimfindeverhalten bzw. die Analyse geflogener Strecken ging. Dies ist vor allem dem Fortschritt in der Beobachtungstechnik zu verdanken. Mittlerweile sind kleine GPS-Geräte verfügbar, die auf dem Rücken der Taube angebracht werden können und mittels derer Parameter wie Streckenlänge, Effizienz (Luftlinienstrecke/geflogene Strecke), Flugdauer, Durchschnittsgeschwindigkeit, Durchschnittsflughöhe, Koordinaten der gesamten Strecke und Geschwindigkeits- und Höhenprofile ermittelt werden können [Steiner et al., 2000]. Diese Untersuchungen erbrachten eine Vielzahl von neuen bzw. vertieften Erkenntnissen über das Flug-, Zug- oder Navigationsverhalten vieler Vogelarten einschließlich der Brieftaube hervor. So weiß man mittlerweile, dass Brieftauben bei Strecken, die ihnen vertraut sind, eine Präferenzroute entwickeln, die bei weiteren Flügen konsequent geflogen wird [Meade et al., 2005]. Dabei folgen die Tiere linearen Landmarken wie Flüssen, Autobahnen oder Eisenbahnlinien, auch wenn das eventuell sogar einen kleinen Umweg bedeutet. Es ist sogar beobachtet worden, dass überflogene Autobahnen bisweilen genau an den entsprechenden Ausfahrten „verlassen“ wurden [Lipp et al., 2004]. Lässt man zwei Tiere mit unterschiedlichen Präferenzrouten gemeinsam auf, so führt dies zu Konflikten, die unterschiedlich gehandhabt werden. Schwarmvögel, wie z.B. Brieftauben, fliegen einerseits gern gemeinsam, andererseits folgen diese Tiere auch gern der gewohnten Strecke. Liegen die beiden Präferenzstrecken nicht so weit auseinander, dann wählen die Tiere eine dazwischen liegende Route und fliegen gemeinsam. Liegen die beiden Präferenzrouten weit auseinander, so setzt sich entweder eine der beiden Tauben durch und beide fliegen deren Präferenzstrecke (was häufiger der Fall ist) oder sie trennen sich und jede fliegt alleine ihre gewohnte Strecke (was seltener der Fall ist) [Biro et al., 2006]. Interessant ist auch, dass sich beim Fliegen in Gruppen die Navigationsleistung verbessert, d.h. es wird bevorzugt ein direkterer Weg geflogen, auch wenn die Einzeltiere allein eigentlich längere Strecken fliegen [Dell’Arriccia et al., 2008]. Alle diese Ergebnisse beziehen sich auf Brieftauben im Allgemeinen und lassen z.B. das Geschlecht der untersuchten Tiere oder auch soziale Parameter wie den Paarungs- oder Brutstatus außer Acht. Brieftauben leben im Schwarm mit einer flexiblen sozialen Struktur. Sie sind monogam und vor allem die männlichen Tiere sind sehr territorial, was den gemeinsamen Nistbereich angeht. Beide Geschlechter sind am Bebrüten der Eier und der Aufzucht der Jungen beteiligt. Das Bebrüten der Eier ist ritualisiert. Etwa von 10-17 Uhr brüten die Täuber, den Rest der Zeit die Täubinnen [Johnston und Janiga, 1995]. Brieftaubenzüchter nutzen diese spezifischen Verhaltensweisen, um bestimmte Strategien zu entwickeln, die bei Wettflügen die

Heimkehrmotivation der Tiere erhöhen sollen. So haben die männlichen Tiere einen festen Nistplatz, den sie intensiv verteidigen. Am Anfang der Wettkampfsaison werden sie mit einem Weibchen verpaart, von diesem dann aber wieder getrennt. Kurz vor dem Wettflug bekommt der Täuber sein Weibchen noch einmal gezeigt oder darf ein paar Minuten mit ihm verbringen. Zudem wird dafür gesorgt, dass die Täubin den Täuber in der Nistzelle erwartet, wenn dieser vom Wettflug zurückkehrt. Eine andere Möglichkeit ist das Einbringen eines möglichen Konkurrenten in den Schlag, kurz bevor die Tiere für einen Wettflug eingefangen werden. Auch das erhöht die Motivation, schnell zurück zu fliegen.

Dieses anekdotische Wissen und die Tatsache, dass alle bisherigen Studien soziale Parameter außer Acht gelassen haben, führen zu der Frage, inwiefern hier ein möglicher sozialbasierter Einfluss auf die Heimkehrleistung bzw. auf die Motivation heimzufliegen besteht. Zur Untersuchung dieser Fragestellung eignet sich am besten die Analyse von für die Tauben bekannten Strecken, da hier die Heimkehrleistung unabhängig von der individuellen Navigationsfähigkeit sein sollte. Wenn jedes Tier den Weg nach Hause kennt, sollten Unterschiede in der Heimfindeleistung durch andere Gründe, wie z.B. die Motivation, bedingt sein. In der nachfolgenden Arbeit [Mehlhorn und Rehkämper, 2016, **Publikation 7**] haben wir uns mit dieser Fragestellung befasst und dazu ein ähnliches experimentelles Design wie Biro et al. [2006] angewendet, die Einzel- und Zweierflüge auf einer vertrauten Strecke mittels GPS-Geräten untersucht haben. Allerdings legten wir unseren Fokus auf soziale Parameter wie das Geschlecht und vor allem den aktuellen Paarungs- und Brutstatus in der Annahme, dass dies motivierende Faktoren für eine direkte Heimkehr sind. Zusätzlich haben wir noch Gruppenflüge durchgeführt, um zu überprüfen, ob sich die Heimkehrleistung bei Gruppen verbessert.

Für diese Untersuchungsreihe wurden 24 Brieftauben (9 Paare und 6 unverpaarte Weibchen) an das Tragen von GPS-Geräten gewöhnt (Abb.14) und für eine Strecke von ca. 10 km Länge trainiert. Alle Tiere waren mindestens ein Jahr alt und hatten bereits Wettflüge von bis zu 300 km Länge in der Vergangenheit absolviert. Um den Brutzyklus zu synchronisieren wurden die Pärchen ein paar Wochen vor Testbeginn getrennt und kurz vor den Tests wieder zusammengeführt. Dann wurde ihnen Gelegenheit gegeben, Eier zu legen und diese auch zu bebrüten. Nach der Gewöhnung an den Auflassort bzw. der Absolvierung von mehreren Einzelflügen wurden verschiedene Paar- und Gruppenkombinationen gebildet und die Tiere schließlich in diesen Kombinationen zusammen aufgelassen. Pro Tier erfolgte jeweils ein Auflass pro Tag. Verpaarte Tauben flogen zuerst mit ihrem Partner und daran anschließend mit einer Taube anderen Geschlechts aus ihrem Schlag, mit der sie aber nicht verpaart waren. Der nächste Auflass erfolgte gleichzeitig mit einer Taube gleichen Geschlechts und der letzte in Sechser-Gruppen mit jeweils drei Pärchen. Die unverpaarten Weibchen absolvierten jeweils drei Zweier-Flüge mit jeweils einem anderen unverpaarten Weibchen und am Schluss ebenfalls einen Gruppenflug. Bei den letzten beiden Auflässen handelte es sich um Gruppenflüge bestehend aus den neun verpaarten Weibchen oder den neun verpaarten Männchen. Während die ersten Auflässe alle randomisiert über den Tag hinweg verteilt stattfanden, wurde nun jede Gruppe jeweils einmal um 8 Uhr morgens und um 14 Uhr aufgelassen, also zu Zeiten, wo entweder die Weibchen (8 Uhr) oder die Männchen (14 Uhr) mit dem Bebrüten der Eier betraut waren. Zudem lagen diese Auflässe am Ende der Brutperiode kurz vor dem erwarteten Schlupfzeitpunkt. Analysiert wurde die Streckeneffizienz, sprich die Differenz zwischen Streckenlänge (Luftlinie) und tatsächlich geflogener Strecke. Ein Effizienzindex von 1 würde somit bedeuten, dass die Taube den direktesten Weg, also Luftlinie geflogen ist, Werte nahe 1 deuten auf eine hohe Streckeneffizienz hin. Aufgrund von physikalischen Unterschieden (die Männchen sind insgesamt signifikant größer bzw. schwerer als die Weibchen, zudem kostet die Eiablage und das Bebrüten zusätzlich Kraft) und den daraus möglicherweise resultierenden Unterschieden in der physischen Leistungsfähigkeit, wurde bewusst auf einen Vergleich der Durchschnittsgeschwindigkeiten der geflogenen Strecken verzichtet.

Abb. 14. Brieftaube (*Columba livia* f.d.) mit einem GPS-Gerät, das auf dem Rücken angebracht ist. Die Bildrechte liegen bei der Autorin.

Alle Tauben eines Auflasses flogen immer zusammen, es erfolgte nie eine Trennung der Tiere. Der statistische Vergleich der Effizienzindices zeigte, dass die unverpaarten Weibchen die höchste Effizienz in den Einzelflügen und Zweierflügen aufwiesen. Generell konnte bei den Gruppenflügen die höchste Effizienz beobachtet werden, gefolgt von den Zweierflügen mit einer Taube des anderen Geschlechts. Zweierflüge mit dem eigenen Partner zeigten die geringste Effizienz. Zudem zeigten die verpaarten Weibchen bei Flügen um 8 Uhr morgens eine statistisch signifikant höhere Effizienz als um 14 Uhr (Abb. 15). Abb. 16 zeigt beispielhaft die mit GPS aufgenommenen geflogenen Strecken eines unverpaarten Weibchens.

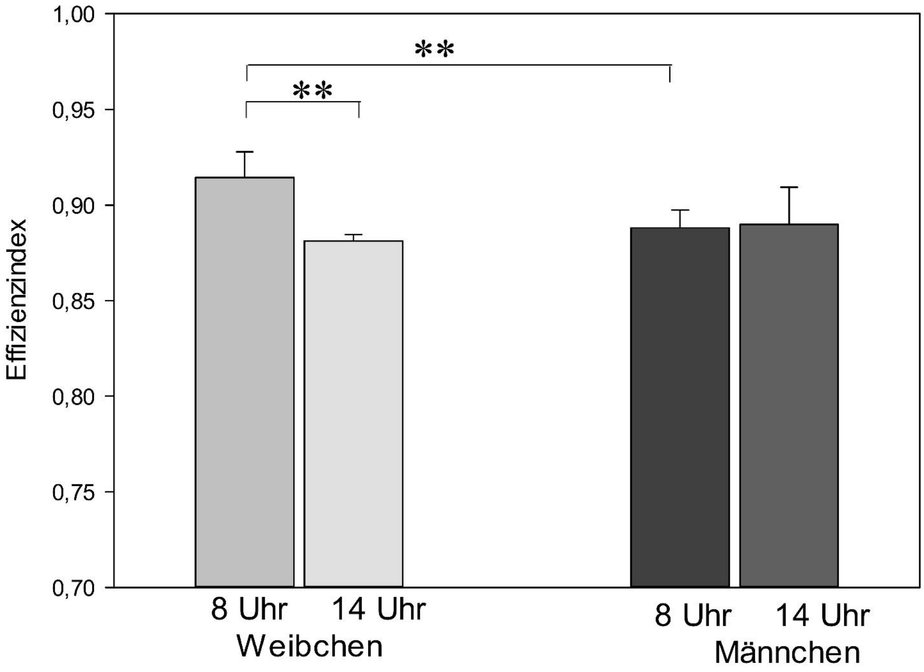


Abb. 15. Effizienzindizes (MW±Stabw) verpaarter und brütender Täuber und Täubinnen zu verschiedenen Auflasszeiten, **p=0.008. Die Bildrechte liegen bei der Autorin (Quelle: Mehlhorn und Rehkämper, 2016).

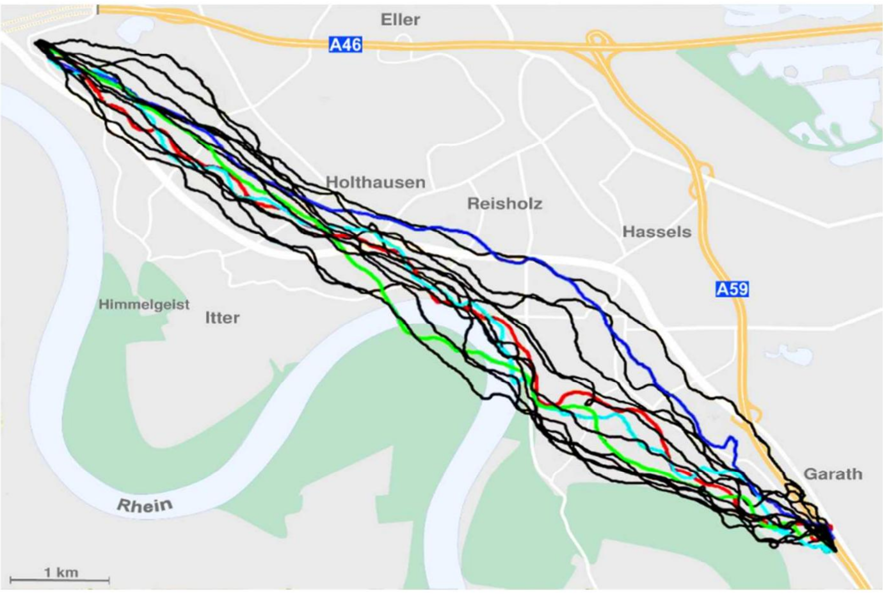


Abb. 16. Beispiel für die Einzel, Zweier- und Gruppenflüge eines unverpaarten Weibchen. Schwarz=Einzelflüge, Rot, Blau, Grün=1., 2. Und 3. Zweierflug, Hellblau= Gruppenflug. Die Bildrechte liegen bei der Autorin (Quelle: Mehlhorn und Rehkämper, 2016).

Aufgrund der Tatsache, dass es während der zu Habituationszwecken durchgeführten ersten Einzelflügen erst zu einem Anstieg der Effizienz kam und diese nach ein paar Tagen stagnierte, konnte davon ausgegangen werden, dass ein charakteristischer Lernprozess stattgefunden hat und weiteres Training keinen Einfluss mehr auf die folgenden Flüge haben würde. Unterschiede in den Effizienzindices sollten nun auf andere Ursachen, wie z.B. eine unterschiedliche Motivation, zurückzuführen sein. Interessanterweise zeigten die unverpaarten Weibchen sowohl in den Einzel- als auch den Zweierflügen die beste Effizienz, so dass Zölibatismus als motivierender Faktor angesehen werden kann. Ebenso hat die Gruppengröße einen motivierenden Effekt, wie die hohen Effizienzindices der Gruppenflüge bei allen Gruppen belegen. Dies steht im Konsens mit den Befunden in der Literatur [Biro et al., 2006; Dell'Arriccia et al., 2008] und wird u.a. mit dem so genannten „many wrong" Prinzip erklärt, nach dem mit steigender Gruppengröße individuelle Fehler in der Navigation ausgemerzt werden [Simons, 2004]. Da dies bei allen Gruppen zu beobachten war, scheinen hier soziale Parameter eine nicht so große Rolle zu spielen. Die erhöhte Effizienz zeigte sich auch schon bei den Zweierflügen, allerdings bilden die Zweierflüge der Pärchen eine Ausnahme. Obwohl zu erwarten gewesen wäre, dass die Effizienz hier besonders hoch sein müsste (da die Nistzelle und das Gelege nun unbewacht bzw. unbetreut sind), scheint hier schon die gemeinsame (Flug-) Zeit mit dem Partner als motivierender Faktor oder als eine Art Belohnung zu agieren, was sich schließlich negativ auf die Heimflugeffizienz auswirkt. Hier wäre es interessant zu untersuchen, wie es sich bei längeren Flügen oder Flügen von unbekannten Auflassorten verhält, wo die Anforderungen an die Tiere viel größer sind und dann auch die Navigationsfähigkeit ein wesentlicher Faktor sein würde. Die letzten hier vorgenommenen Auflässe machten deutlich, dass der Brutstatus ebenfalls einen motivierenden Effekt auf das Flugverhalten hat. Dies ist aber vor allem bei den Weibchen zu beobachten und kann mit dem größeren Investment der Weibchen bezüglich der Eiablage und der Brutzeiten erklärt werden [Parker et al., 1972]. Ein existierendes Gelege und ein bevorstehender Schlupf steigern (zumindest bei den Weibchen und bei bekannten Strecken) die Motivation, auf direktem Wege zum Schlag zurückzufliegen.

Bei der Untersuchung des Heimfindeverhaltens oder des Navigationsverhaltens von Vögeln ist schon aufgrund von unterschiedlichen Wetterlagen oder den unterschiedlichen Begebenheiten verschiedener Auflassorte eine Reproduzierbarkeit oder das Treffen von allgemeingültigen Aussagen schwierig. Nichts desto trotz kann die Analyse von geflogenen Strecken interessante Einblicke in den Heimfindeprozess liefern. Unsere diesbezügliche Studie ermöglichte einen Einblick über den Einfluss von Parametern, die nichts mit der Navigationsleistung im engeren Sinn zu tun haben. Soziale Parameter könnten hier eine größere Rolle spielen als bisher gedacht und sich erheblich auf die Heimkehrmotivation und dadurch letztendlich auf die Heimkehrleistung auswirken. Dies ist ein Gesichtspunkt, der bei der Evaluation und Interpretation von Flugdaten generell beachtet werden sollte, vor allem aber dann, wenn es sich um Daten von experimentell manipulierten Tieren handelt. Hier muss bei einer schlechteren Heimkehrleistung hinterfragt werden, ob wirklich der experimentelle Eingriff oder generell das experimentelle Design zu einer reduzierten Heimkehrleistung geführt haben, oder vielleicht einfach eine reduzierte Motivation, nach Hause zu fliegen.

VII Übergreifende Betrachtung

In den letzten Jahrzehnten haben zahlreiche Untersuchungen zeigen können, dass viele Taxa (Vögel, Cephalopoden u.a.) ohne einen typischen „sechs-schichtigen“ Neocortex komplexes, intelligentes Verhalten und kognitive Fähigkeiten besitzen, die vergleichbar sind mit denen von Säugern und diese manchmal sogar übertreffen. Gemeinsam ist all diesen kognitiven Funktionen und Fähigkeiten, dass sie auf Regelkreisen basieren, die artübergreifend überraschend ähnlich sind. Trotzdem zeigen natürlich auch Vögel artspezifische Besonderheiten in ihrem Hirnbau, die ihre Lebensweise, Verhaltensweisen und kognitiven Fähigkeiten widerspiegeln. Bei den hier untersuchten Neukaledonienkrähen und Brieftauben zeigen sich diese Unterschiede schon makroskopisch in der unterschiedlich starken Ausgestaltung des Telencephalons (Abb. 17), wobei das der Neukaledonienkrähe viel größer ist. Die hier beschriebenen Untersuchungen belegen auch einige mikroskopische und zahlreiche volumetrische Unterschiede. Neukaledonienkrähen und Brieftauben unterscheiden sich signifikant in ihrer Hirn-Körpergewichtsbeziehung (unter Berücksichtigung der Portmanndaten (siehe **Publikation 1** bzw. Cnotka et al., 2008a)). So haben Neukaledonienkrähen einen Encephalisationsindex von 2,32 und Felsentauben von 0,68; die Brieftauben liegen noch etwas darunter (siehe Rehkämper et al., 2008) und auch sonst gibt es einige Unterschiede im Hirnbau, was aufgrund der unterschiedlichen Lebensweise und den stark differierenden Verhaltensweisen inklusive kognitiver Eigenschaften auch nicht verwundert. Beide Tiere besitzen auf ihre Art und Weise herausragende kognitive Fähigkeiten. Die Neukaledonienkrähen mit ihrer Fähigkeit zur Werkzeugherstellung und deren Gebrauch sowie ihrem Vermögen, kausale Zusammenhänge zu begreifen und die Brieftauben durch ihre herausragenden Orientierungs- und Navigationsfähigkeiten. Dementsprechend liegt im Gehirn der Neukaledonienkrähe eine Konzentration auf assoziative Vorderhirnareale wie dem Mesopallium vor und im Gehirn der Brieftauben eine Konzentration auf Regionen zur räumlichen Wahrnehmung wie dem Hippocampus oder sinnesverarbeitenden Strukturen wie dem Bulbus olfactorius, sowie - in Bezug auf die Lateralisation - auf dem Wulst. Die morphometrisch erfassbare Hirnanatomie von Neukaledonienkrähen und Brieftauben kann als adaptives Spiegelbild ihrer Verhaltenseigenarten angesehen werden.

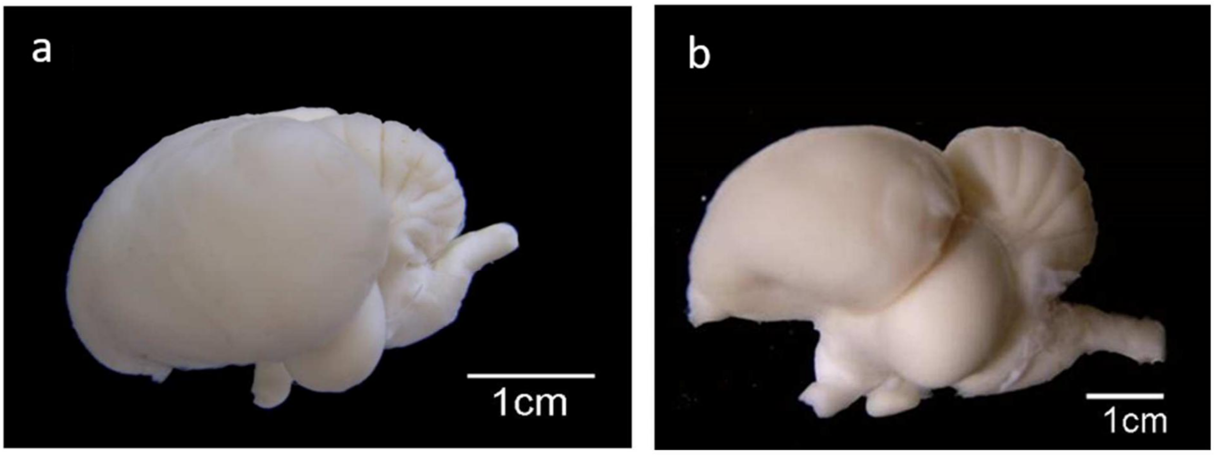


Abb.17. Die Gehirne einer Neukaledonienkrähe (a) und Brieftaube (b) in Seitenansicht. Die Bildrechte liegen bei der Autorin.

Werkzeuggebrauch wird nicht immer als Indikator für besondere kognitive Fähigkeiten diskutiert. Viele Wirbeltiere und auch wirbellose Tiere benutzen Werkzeuge in irgendeiner Art und Weise [Beck, 1980; Hansell, 2007]. Das hat eher selten etwas mit kognitiven Fähigkeiten zu tun und wird auf einige wenige Schlüsselreize zurückgeführt, die ebenso angeboren sind wie ihre Reaktion darauf. Beispiele sind die Konstruktion von Bauten, Netzen o.ä. [Hansell, 2007]. Demgegenüber ist der Werkzeuggebrauch bei Primaten und einigen Vögeln mit kognitiver Flexibilität assoziiert, sollte aber nicht per se als ein Indikator für hohes kognitives Können (mit entsprechendem Hirnbau) angesehen werden.

Bei den Brieftauben sind die Leistungen in puncto räumlicher Kognition umso beeindruckender, da diese Tiere als niedrig encephalisiert gelten, was man spontan mit geringer kognitiver Kapazität verbinden würde. In den hier vorgelegten Arbeiten konnte dagegen gezeigt werden, dass kognitive Fähigkeiten nicht mit einem großen Gehirn respektive großen Telencephalon einhergehen müssen, sondern eine Vergrößerung/Anpassung von kognitionsspezifischen Strukturen, wie dem Hippocampus, und entsprechender sinnesverarbeitender Strukturen ausreicht. Zwar sind sicherlich auch assoziative Hirnstrukturen wie das Mesopallium an der Verarbeitung räumlicher Informationen beteiligt, allerdings nicht in einem Ausmaß, der sich morphologisch bzw. volumetrisch belegen lässt bzw. sich nur dahingehend zeigt, dass hier anscheinend eine Lateralisation funktionelle Vorteile zu haben scheint.

Die beschriebenen Arbeiten dokumentieren einen deutlichen Einfluss von Erfahrung auf das (Brieftauben-) Gehirn bzw. die Hirnregionen, die an der räumlichen Wahrnehmung beteiligt sind (inklusive Hemisphärenunterschieden) wie auch direkt auf die räumliche Kognition. Entsprechende Untersuchungen über den Einfluss von Erfahrung auf das Gehirn der Neukaledonienkrähen und deren kognitiven Leistungen fehlen bisher, sind aber erforderlich und wären sicher sehr aufschlussreich. So ist bekannt, dass die Krähen mit fortschreitender Erfahrung immer versierter in der Herstellung von Werkzeugen und deren Gebrauch werden und diese Fertigkeiten auch an ihre Nachkommen weitergeben [Hunt und Gray, 2003; Kenward et al., 2005]. Die Befunde der hier vorgelegten Arbeiten deuten darauf hin, dass es eine wechselseitige Beziehung zwischen Erfahrung (bzw. individueller Lebensgeschichte) und Hirnstrukturgröße gibt. Dies bezieht sich nicht nur auf domestizierte Tiere wie die Brieftaube, sondern ist auch bereits bei Wildtieren beobachtet worden [Clayton und Krebs, 1994]. Ein weiterer spannender Aspekt ist die Betrachtung der Lateralisation der Gehirne von Neukaledonienkrähen und Brieftauben. Mehlhorn et al. [2010b, 2017] zeigten sowohl morphologische, als auch funktionelle Asymmetrien im Gehirn der Brieftaube. Interessanterweise lässt sich bei den Neukaledonienkrähen keine (morphologische) Lateralisation feststellen (unveröffentlichte Daten). Allerdings gibt es einzelne Untersuchungen zu funktionellen Spezialisierungen in Bezug auf einen Werkzeuggebrauch, der vergleichbar ist mit unserer „Händigkeit“ [Hunt et al, 2006; Weir et al., 2004]. Dies deutet darauf hin, dass sich nicht alle Spezialisierungen/Lateralisationen volumetrisch zeigen müssen, schließt jedoch nicht aus, dass es vielleicht andere weitere morphologische Parameter gibt, die die neuronale Grundlage der beobachteten funktionellen Lateralisationen sein könnten (z.B. Neuronendichte, Rezeptorenanzahl, Ausprägung der Faserbahnen etc.).

Befunde, die den Einfluss von Erfahrung auf das Gehirn zeigen, haben zwangsläufig auch Auswirkungen auf eine Evolutionstheorie, die besagt, dass Struktur-Funktions-Korrelationen auf vererbbaren Komponenten basieren, die sich im Sinne der adaptiven Selektion als vorteilhaft in der Evolution erwiesen. Dem würden unsere Befunde widersprechen. Dafür könnten sie im Einklang stehen mit der erstmalig von Maynard Smith [1982] vorgestellten evolutionären Spieltheorie [Mehlhorn und Rehkämper, 2010]. Der Grundstein der Spieltheorie basiert auf der so genannten „Strategie“, welche ein morphologisches, physiologisches oder ethologisches Merkmal darstellt, das sich in Konkurrenz zu einem anderen Merkmal als erfolgreicher in Bezug auf die Anzahl und/oder Fitness der Nachkommenschaft erweist. Im traditionellen Sinne ist diese Strategie bzw. dieses Merkmal vererbbar, aber im Falle der Neuroanatomie ist es durchaus denkbar, dass diese Strategie sowohl aus vererbbaren als auch nicht vererbbaren Teilen besteht. Die Relevanz der individuellen Erfahrung muss signifikant sein und auch das Potential ihrer Modifizierungsmöglichkeiten muss völlig ausgeschöpft werden, damit eine Weitergabe an die nächste Generation gewährleistet ist. Wenn eine genetische Prädisposition für Lernen (oder Navigation) vorausgesetzt wird, wie es unsere Untersuchungen an Brieftauben nahelegen, so ist es notwendig, dass dieses genetische Potential auch voll genutzt wird und es z.B. durch Erfahrung zur vollen Ausprägung kommt/kommen kann. Dadurch könnte es zu einem höheren Fortpflanzungserfolg führen und somit indirekt an die nächste Generation weitergegeben werden.

Die relative Hirn-(teil) Größe als Maß für Intelligenz bzw. kognitive Fähigkeiten legte zwar den Grundstein für komparative Betrachtungen, mittlerweile erlauben neuere Techniken hier jedoch auch weitere Einblicke. So wird seit einigen Jahren vorgeschlagen, dass die Neuronenzahl, die sich mittlerweile relativ präzise bestimmen lässt, womöglich besser geeignet sei, um artspezifische (kognitive) Fähigkeiten zu beurteilen [Olkowicz et al., 2016; Herculano-Houzel, 2017]. Dazu passt, dass unter den Säugetieren generell die Primaten und hier vor allem die Menschenaffen die relativ höchste Anzahl an Neuronen aufweisen, mit dem Höchstwert beim Menschen [Herculano-Houzel et al., 2015]. Interessanterweise zeigte sich, dass die Neuronenzahl pro definierter Hirneinheit bei Vögeln weitaus höher ist als bisher angenommen. So erreichen z.B. einige Papageien- und Singvogelarten im relativen Vergleich zu Primaten mehr als doppelt so hohe Werte [Olkowicz et al., 2015]. Dass Papageien und Singvögel nun doppelt so intelligent sind wie Primaten bzw. doppelt so große kognitive Fähigkeiten aufweisen, ist sicher nicht richtig. Es scheint daher der Fall zu sein, dass eine hohe Neuronenzahl zur Grundausstattung der Vögel gehört und hier artspezifisch variieren kann. Ob die Neuronenzahl innerhalb der Klasse *Aves* in jedem Fall Aufschluss über die kognitiven Fähigkeiten geben kann, muss ebenfalls in Frage gestellt werden. Zwar passt ins Bild, dass Corviden eine sehr hohe Neuronenzahl aufweisen, was ihre besonderen Fähigkeiten erklären könnte. Diese Schlussfolgerung trägt aber nicht bei Tauben. Bei ihnen ist die Neuronenzahl relativ gering [Olkowicz et al., 2015]. Zudem konnten schon Delius und Habers in den 70er Jahren des 20. Jahrhunderts [1978] zeigen, dass Tauben in Bezug auf ihre visuelle Wahrnehmung zur Abstraktion fähig sind, was damals exklusiv als eine dem Menschen vorbehaltene kognitive Kompetenz galt. Güntürkün et al. [2017] zeigten erst kürzlich, dass die Leistungen in einigen allgemeinen kognitiven Fähigkeiten (wie z.B. Kurzzeitgedächtnis, orthographische Verarbeitung und abstraktes Zahlenverständnis) von Tauben und Corviden (und sogar Affen) gar nicht so weit auseinanderliegen wie erwartet. Dass die Fähigkeiten zur räumlichen Kognition der Tauben die der Krähen um ein Vielfaches übertreffen, ist unbestritten. Auch darf nicht außer Acht gelassen werden, dass sich viele kognitive Fähigkeiten (wie z.B. die Objektpermanenz oder die Selbsterkennung im Spiegel (als Nachweis für ein Bewusstsein des eigenen Selbst) trainieren bzw. erlernen lassen (auch von Tauben) und eine hohe Lernfähigkeit ebenfalls eine kognitive Leistung ist. Es ist daher davon abzuraten, eine generelle Rangfolge zwischen verschiedenen (Vogel-) Arten bzw. ihren kognitiven Fähigkeiten anzustellen, sondern vielmehr zu fordern, genau zu definieren, um welche kognitive Leistung es sich im Einzelnen handelt. Dabei sind die entsprechenden Fähigkeiten auf ihre "Kognitivität" zu diskutieren. Eine hohe Neuronenzahl ist hier kein Indikator für höhere oder bessere Leistung, hilft aber offenbar bei der schnelleren Umsetzung von kognitiven Fähigkeiten und ermöglicht ein schnelleres und flexibleres Lernen vor allem in Bezug auf neue Situationen [Güntürkün et al., 2017].

Zusammenfassend haben die vorgelegten Arbeiten gezeigt, dass sich sowohl Neukaledonienkrähen, als auch Brieftauben als Modellorganismen für kombinierte Untersuchungen der Neuro- und Kognitionswissenschaften eignen. Sie erhellen kausale Zusammenhänge zwischen der Morphologie des Gehirns und seiner Funktion bei den untersuchten Formen. Dadurch wurden und werden Erkenntnisse grundlegender Art gewonnen, die letztlich durch die Homologien zwischen Vogel- und Säugergehirn und die Ähnlichkeit diverser neuronaler Mechanismen gerade in Bezug auf Lernen und Handlungssteuerung im Sinne translationaler Neurowissenschaften auch zum Verständnis des menschlichen Gehirns beitragen können.

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Extraordinary large brains in tool-using New Caledonian crows (*Corvus moneduloides*)

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Abstract

A general correlation exists between brain weight and higher cognitive ability in birds and mammals. In birds this relationship is especially evident in corvids. These animals are well-known for their flexible behavior and problem-solving abilities, and have relatively large brains associated with a pallial enlargement. At the behavioral level, New Caledonian crows stand out amongst corvids because of their impressive object manipulation skills both in the wild and in the laboratory. However, nothing is known about the relative size of their brains. Here we show that NC crows have highly encephalised brains relative to most other birds that have been studied. We compared the relative brain size of five NC crows with combined data for four passerine species (7 European carrion crows, 2 European magpies, 3 European jays and 4 domestic sparrows) and found that NC crows had significantly larger brains. A comparison only with the seven carrion crows also revealed significantly larger brains for NC crows. When compared with brain data for 140 avian species from the literature, the NC crow had one of the highest degrees of encephalisation, exceeding that of the 7 other Corvidae in the data set.

Keywords: New Caledonian crow; *Corvus moneduloides*; Brain; Brain size; Cognition

Avian species belonging to the order Passeriformes have relatively large brains in comparison to the other birds [38]. This is especially true for the Corvidae family. It has been suggested that the encephalisation in Corvidae is related to their flexible behavior and considerable learning abilities [4,24,43,41,49]. *Corvus* species, in particular, are highly innovative (for review see Ref. [34] and Table 1 in Ref. [32]), can manufacture tools (*Corvus moneduloides* [20]), spontaneously solve novel problems (*Corvus corax* [18,19]; *C. moneduloides* [55]), use tactical deception (*C. corax* [6]) and can learn from conspecifics (*C. corax* [13]). In fact, there is increasing evidence that they independently evolved brains and associated cognitive abilities similar to those of primates [12,39]. The New Caledonian crow (NC crow hereafter, *C. moneduloides*, Fig. 1) stands out amongst corvids because of its impressive tool manufacturing skills in the wild [20–23]. NC crows have also exhibited considerable problem-solving skills in the laboratory comparable to those of nonhuman primates [55–57].

A large number of studies show that higher cognitive abilities correlate with larger relative brain size in both mammals [2,16,51] and birds [24,32,34,37,38,41]. To see if this was the case with NC crows, we first compared the relative brain weight of the NC crow with that of four other Passeriformes (European carrion crow *Corvus c. corone*, European magpie *Pica pica*, European jay *Garrulus glandarius* and domestic sparrow *Passer domesticus*) using the same histological procedure (individual body weight and brain weight of perfused birds). As data for comparably treated birds are lacking, we also compared our NC crow brain data with fresh brain weights for a wide range of avian species using the largest set of data available [38].

Our study material consisted of the perfused brains of five NC crows, seven European carrion crows, two European magpies, three European jays and four domestic sparrows. All the birds were captured in their original habitat and weighed immediately after catching to determine body weights. The five NC crows were kept in an outdoor aviary for one week before being

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Fig. 1. New Caledonian crow holding a leaf–stem tool.

euthanized. The crows were provided with food twice daily and permanent, clean water while in the aviary.

All the 21 birds above were euthanized with an overdose of pent barbiturate then weighed again. After cardiac arrest was confirmed they were perfused with physiological saline solution to wash out the blood, followed by Bodian's fluid to fix the brain [46]. The brains were removed immediately following the perfusion process to ensure that they were not significantly different from fresh brain weights [50]. Thus, a correction for shrinkage due to fixation was not necessary.

Brain weight scales allometrically with body weight [7,48,53], therefore allometric methods were used. The relationship between brain and body weight is represented best by the allometric formula: $\log y = \log b + a \log x$ where y represents the brain weight, b the intercept of the allometric regression with the abscissa, x the body weight and a the slope of the regression [48].

We compared the brain weight of NC crows to that of other birds by carrying out three regression analyses. Ideally these analyses would be conducted taking into account phylogenetic relationships [17]. Unfortunately, no character-based phylogeny has been published for *Corvus* and thus no phylogenetic corrections are possible. The first regression used material from our collection, which consisted of 21 brains from 5 passerine species. Portmann [38] provides the largest published set of fresh brain and body weights, containing data for 140 individual species (given as species means without error statistics). Thus, we also combined our brain data for the NC crow with those of Portmann's to see how brain size of the NC crow compared to birds in general. We carried out the remaining two regressions using this data set. The first of these two regressions included all of Portmann's 140 species and our NC crow data, and the second included only Corvidae species. Portmann's data set included seven Corvidae species [47]: the common raven (*C. corax*), the European carrion crow (*Corvus c. corone*), the rook (*Corvus frugilegus*), the European magpie (*P. pica*), the jackdaw (*Corvus monedula*), the red billed chough (*Pyrrhocorax pyrrhocorax*) and the European jay (*Garrulus glandarius*).

To analyze the differences in relative brain size between the 5 New Caledonian crows and the 16 other perfused passerines (from our own collection, see above), we calculated allometric encephalisation indices (E). To calculate the indices we divided the actual brain size of an individual by its predicted brain size obtained from the regression [50]. All points on the regression line represent an E of 1.0, so an E of 2.0 would mean that a brain was twice as heavy as the predicted weight based on the data. We used the t-test to compare encephalisation indices.

To detect outliers in the two regressions using Portmann's [38] data we examined the studentized residuals. Studentized residuals are distributed as a t distribution with $n-3$ degrees of freedom for simple regression [3]. Therefore, we can approximately determine if an individual residual is statistically significant or not. In other words, we can test if the corresponding observation conforms to the regression model that describes the other observations.

The five NC crows had a mean body weight of 277.25 ± 29.87 g (mean ± S.D.) and a mean perfused brain weight of 7.56 ± 0.77 g. The mean encephalisation index (1.103 ± 0.158) for the 5 NC crows was significantly greater than the mean for the 16 other passerines (0.974 ± 0.072; $t = -2.603$, d.f. = 19, $p = 0.017$, Figs. 2 and 3). The mean encephalisation index for the NC crows was also significantly greater than that for the seven European carrion crows (0.939 ± 0.047; $t = 2.641$, d.f. = 10, $p = 0.025$).

When data for the NC crow was plotted with Portmann's 140 species (Fig. 4), 9 species had studentized residuals larger than $t = 1.656$ (the 1-tailed 0.05 significance level for a positive studentized residual in the regression; d.f. = 138). The nine species consisted of a woodpecker (**Piciformes**), five parrots (Psittaci-

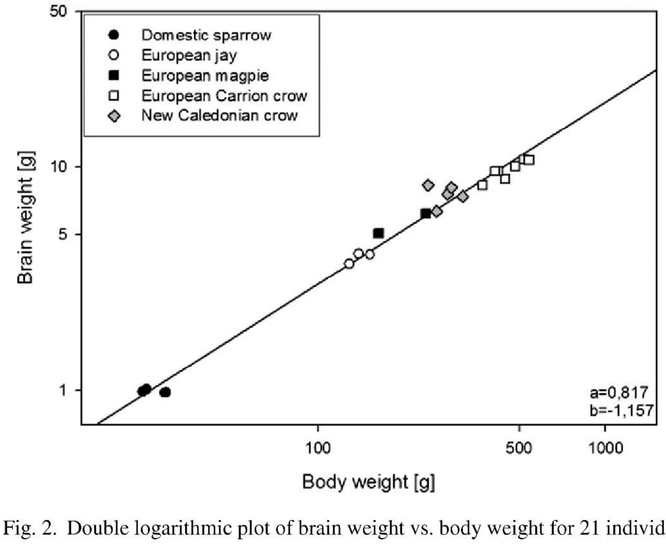

Fig. 2. Double logarithmic plot of brain weight vs. body weight for 21 individuals from 5 passerine species.

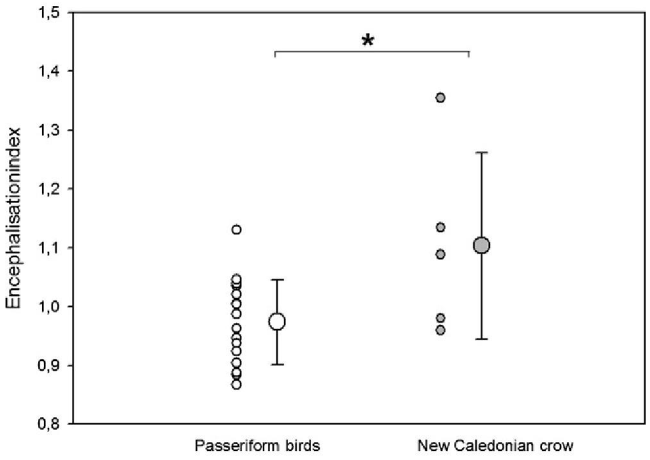

Fig. 3. Encephalisation indices for 16 individuals from 4 passerine species (European carrion crow, European magpie, European jay, domestic sparrow) compared to the indices for 5 NC crows. Individual data with mean and standard deviation are given. $^*p = 0.017$. The error bars are offset from the data points for clarity.

formes), an owl (Strigiformes) and two Corvidae (the NC crow and the common raven). The NC crow had the fourth highest relative brain weight (Fig. 4). Only two Psittaciformes species (the blue and yellow macaw, *Ara arauna*, and the red and green macaw, *Ara chloroptera*) and the black woodpecker (*Dryocopus martius*) had a larger studentized residual (t_S: NC crows = 2.064; *A. arauna* = 2.728; *A. chloroptera* = 2.673; *D. martius* = 2.077). When data for the NC crow were plotted with those for the seven other Corvidae in Portmann's data set, the NC crow was a significant outlier; it was the only species with a t_S-value (2.164) higher than $t = 2.015$ (the 1-tailed 0.05 significance level for a positive studentized residual in the regression; d.f. = 5). These results suggest that the degree of encephalisation in the NC crow is inconsistent with that observed in birds generally and in its close relatives in particular.

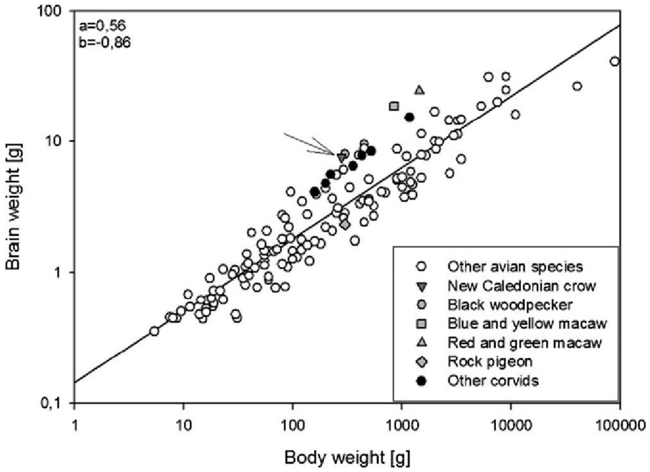

Fig. 4. Double logarithmic plot of brain weight vs. body weight for 141 avian species. Data for the NC crow are the authors' and those for all other species are taken from Portmann (1947). One symbol indicates one species. The arrow indicates the symbol for the NC crow. Given that pigeons are commonly used in behavioral and neuroscience studies, the position of the rock pigeon (*Columba livia*) is also shown.

The present study reveals that the brains of NC crows are probably relatively larger than those of other birds, except for a small number of non-passerine species. Therefore, NC crows' exceptional skills are associated with one of the highest encephalisation values in avian species studied so far. This is consistent with studies that show a positive correlation between brain (component) size and brain (component) function (e.g., Refs. [4,24,44,40,54]). A large number of findings using dozen of species make it likely that ecoethological adaptations and higher cognitive abilities correlate with larger brain size in both mammals [2,16,51] and birds [24,33,37,38,43].

Early on in comparative neuroanatomy, birds were considered to be poorly encephalised and only capable of instinctive behavior [11]. This was mostly because they were thought to lack a cortex but have a hypertrophied striatal area [1]—an opinion that was also reflected in the older terminology of the avian brain [31,35]. It is now generally accepted that most of the avian telencephalon consists of a pallium that is structurally different from, but homologous to, that of mammals [14,29,39]. This paradigm shift also resulted in a new nomenclature of the avian forebrain [28,45].

Brain size of a species (or an individual) is only relevant within a comparative framework. Brain and body weights of newly captured wild animals are ideal, but these data are rare. Portmann [37,38] published a large contingent of brain/body-weight data that covered 140 avian species. Ebinger and collaborators have published such data on rock doves, wild mallards and wild turkeys [8–10] and Rehkämper et al. [43] and Boire and Baron [5] on several other orders of birds (e.g., Galliformes, Passeriformes). Iwaniuk and collaborators have also published avian brain and body-weight data for a large number of species and individuals [25–27]. Most of the brain data are based on endocranial volumes. These data allow a detailed comparison across species and provide new insights into the evolution of the avian brain. However, endocranial volumes and fresh brain weights are not directly comparable. Therefore, we used Portmann's and Rehkämper et al.'s fresh brain/body-weight data to compare the brain weight of NC crows with that for a wide range of other avian species.

Large brains can result from a mosaic-like pattern of selective relative growth of brain components [26,42]. In non-passerines like woodpeckers, total brain size is disproportionally increased by a progressive development of the cerebellum [54]. This is quite different from passerines and (non-passerine) parrots, where encephalisation has largely occurred by an increase of the pallium. Parrots are also capable of impressive cognitive abilities and complex social interactions [36], and both parrots and corvids possess much larger nidopallium and mesopallium proportions than other birds [24,52,43].

Both the nido- and the mesopallium of birds are associative forebrain areas [30,39] that are involved in cognitive functions like flexibility, working memory, and context integration [14,15]. The ability of NC crows to solve complex novel problems demonstrates considerable behavioral flexibility [55–57]. Thus, their impressive skills would seem to require cognitive abilities that are known to be processed within the avian mesopallium and nidopallium. Enlargement of these pallial components and therefore, concomitantly, of total brain weight is a possible explanation for the high degree of encephalisation that we found in NC crows.

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Tool-Making New Caledonian Crows Have Large Associative Brain Areas

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Brain · Brain size · Cognition · *Corvus moneduloides* · Mesopallium · New Caledonian crow · Striatopallidal complex · Tool making · Tool use

Abstract

Animals with a high rate of innovative and associative-based behavior usually have large brains. New Caledonian (NC) crows stand out due to their tool manufacture, their generalized problem-solving abilities and an extremely high degree of encephalization. It is generally assumed that this increased brain size is due to the ability to process, associate and memorize diverse stimuli, thereby enhancing the propensity to invent new and complex behaviors in adaptive ways. However, this premise lacks firm empirical support since encephalization could also result from an increase of only perceptual and/or motor areas. Here, we compared the brain structures of NC crows with those of carrion crows, jays and sparrows. The brains of NC crows were characterized by a relatively large mesopallium, striatopallidal complex, septum and tegmentum. These structures mostly deal with association and motor-learning. This supports the hypothesis that the evolution of innovative or complex behavior requires a brain composition that increases the ability to associate and memorize diverse stimuli in order to execute complex motor output. Since apes show a similar correlation of cerebral growth and cognitive abilities, the evolution of advanced cognitive skills appears to have evolved independently in birds and mammals but with a similar neural orchestration.

Introduction

Higher cognitive abilities have been linked to increased brain size in mammals. These superior abilities are reflected in different domains such as tool use [Reader and Laland, 2002], social skills [Byrne and Corp, 2004] and behavioral flexibility [Sol et al., 2008]. Higher levels of behavioral flexibility also correlate with increased brain size in birds [Portmann, 1946; Lefebvre et al., 1997; Iwaniuk et al., 2004; Cnotka et al., 2008]. The volume of certain associative pallial structures in the avian forebrain are especially good predictors of innovative foraging behavior and tool use [Timmermanns et al., 2000; Lefebvre et al., 2002, 2004; Lefebvre and Sol, 2008]. Among the class of birds

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(Aves), the corvid family is especially renowned for their flexible behavior and cognitive skills [Rehkämper et al., 1991; Iwaniuk and Hurd, 2005; Sol et al., 2005]. New Caledonian (NC) crows *(Corvus moneduloides)* display extraordinary skills in making and using tools to acquire otherwise unobtainable food [Hunt, 1996; Hunt and Gray, 2003, 2004]. These birds manufacture an impressive range of both stick and leaf tools [Hunt and Gray, 2002, 2003, 2004a], may have evolved rudimentary cumulative technology [Hunt and Gray, 2003] and can bend unfamiliar material like wire into functional tools [Weir et al., 2002]. NC crows can also use one tool to get another (metatool use) [Taylor et al., 2007] and solve complex physical cognition tasks that require causal reasoning [Taylor et al., 2009]. These skills rival those of apes [Emery and Clayton, 2004; Emery, 2006].

NC crows have one of the largest avian brains for their body size [Cnotka et al., 2008]. However, when brains evolve to a larger size it is mostly by a differential increase in certain areas and not by a change in the size of all areas, which means that encephalization can result from a mosaic-like pattern of differential growth of brain components [Rehkämper et al., 2001; Iwaniuk et al., 2004; Rehkämper et al., 2008]. Thus, an investigation of the association between encephalization and cognitive skills requires the comparative analysis of separate brain structures. In a first attempt to identify which parts of the NC crow's brain are larger than in other birds, we compared the volume of 15 brain areas between NC crows and three other passerine species [carrion crows *(Corvus corone corone)*, European jays *(Garrulus glandarius)* and domestic sparrows *(Passer domesticus)*]. Among birds, Passeriformes in general have relatively large brains and telencephalic volumes [Rehkämper et al., 1991; Burish et al., 2004; Iwaniuk and Hurd, 2005]. The size of the nidopallium is the best predictor of 'true' tool use [Lefebvre et al., 2002]; therefore this structure in NC crows should be relatively large when compared to non-tool users. However, the size of the mesopallium is the best predictor of behavioral innovation and flexibility generally in birds [Timmermanns et al., 2000]. The high level of tool skills in NC crows (e.g. their manufacture and use of hooks) and their demonstrated cognitive ability in tool- and non-tool-related experiments suggest that their behavior is based on a high level of cognitive ability generally. Therefore, we also predicted that the mesopallium in NC crows would be relatively enlarged. As well as the mesopallium and the nidopallium, we investigated if other associative areas such as the striatopallidal complex showed differential size increase in the NC crow.

Material and Methods

Subjects

We collected the brains of 5 NC crows *(Corvus moneduloides)*, 5 European carrion crows *(C. corone corone)*, 2 European jays *(G. glandarius)* and 4 sparrows *(P. domesticus)*. All the animals were captured in their original habitat and weighed immediately after capture.

Brain Collection

The 16 individuals were euthanized with an overdose of pentobarbital. After cardiac arrest was confirmed, they were perfused with physiological saline solution and a fixative (Bodian's fluid). The brains were carefully dissected, weighed, sectioned and stained for perikarya. We determined total brain volume and the volume of 15 distinct areas: hyperpallium apicale, hyperpallium densocellulare, mesopallium, nidopallium, arcopallium, entopallium, striatopallidal complex (including the globus pallidus, lateral striatum, medial striatum and the tuberculum olfactorium), septum, hippocampus, bulbus olfactorius, tegmentum (this was the brain part caudal to the diencephalon including the medulla oblongata, but excluded the tectum and cerebellum), cerebellum, tectum opticum, tractus opticus and diencephalon. For carrion crows, jays and sparrows, volumetric data other than for the arco- and entopallium were taken from Rehkämper et al. [1991]; we measured the arco- and entopallium from the brain slides used in the 1991 paper.

Analyses

Net brain volume was calculated as the sum of the single brain components. In contrast to total brain volume, the net brain volume does not include the volume of leptomeninges, ventricles, choroid plexus and remains of brain nerves. The nidopallium includes the basal nucleus and field L, and the arcopallium includes the nucleus taeniae amygdalae and parts of the tractus occipitomesencephalicus.

To compare volumes of brain structures in different species with different body weights, allometric methods were used. This involved the calculation of a regression line that expressed the brain (or brain component) size/body weight relationship. We used body weight to account for body size variation because of the well-proven correlation between brain (structure) size and body weight [Snell, 1892; Dubois, 1897; Stephan et al., 1986, 1988; Rehkämper et al., 1991; Baron et al., 1996]. Alternative means of accounting for variation in body size such as using net brain volume or brain stem volume were unsuitable because we wanted to investigate possible enlargement in these parts as well.

To obtain a reliable regression slope for passerines, the body weight range between the smallest and largest species should ideally be a factor of 10; the body weight range for the four species in our study met this criteria. The species that we used to calculate the regression line were also part of a biologically appropriate group, the order Passeriformes [Sibley and Alquist, 1990]. The slopes of brain (or brain component) size/body weight relations were calculated according to the formula:

$$\log \textit{brain (or brain component) size} = \log b + a \times \log \textit{body weight}$$

where 'a' is the slope and 'b' the intersection with the y axis. Regression lines were calculated for each brain structure using data points for all 16 individuals [Warton et al., 2006].

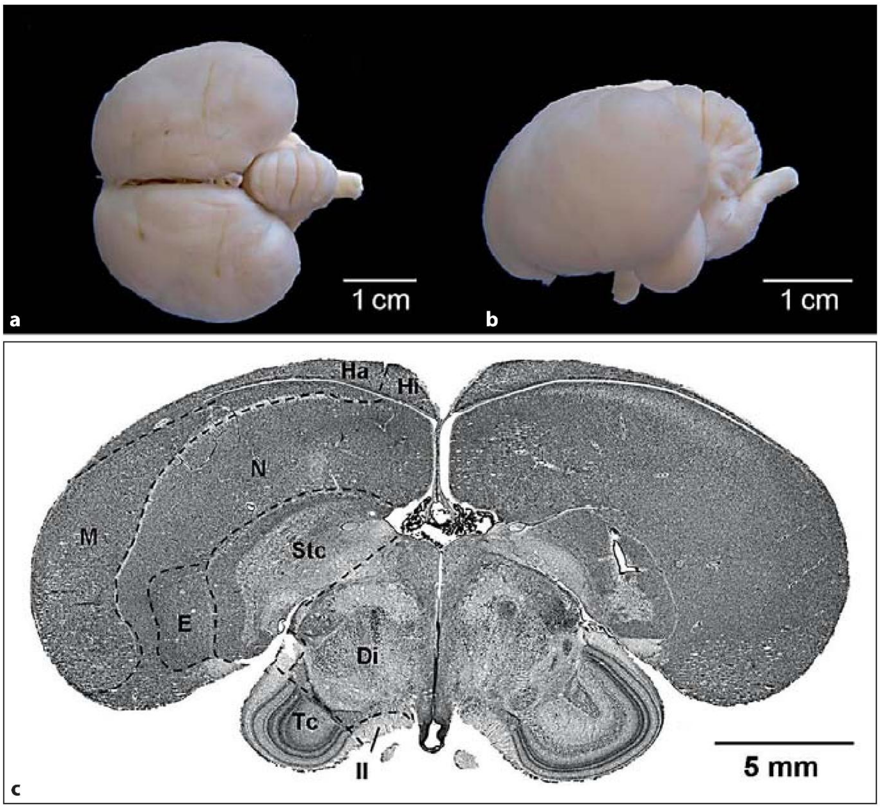

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Fig. 1. The brain of the NC crow. **a**, **b** Lateral and dorsal view of an NC crow brain. **c** Coronal section through the brain of a NC crow to illustrate some subdivisions. Di = Diencephalon; E = entopallium; Ha = hyperpallium apicale; Hi = hippocampus; M = mesopallium; N = nidopallium; Stc = striatopallidal complex; Tc = tectum opticum; II = tractus opticus. Gallyas stain.

To test for differences in brain structure volumes between species we calculated allometric size indices (actual brain component size/expected brain component size). The indices represent the distance of individual data points from the regression line. The expected brain (or brain component) size is the value on the regression line that corresponds to a given individual body weight. The methods that we used for the preparation of brain material, establishing boundaries between brain areas, measurements and for allometric calculations are taken from the literature [Stokes et al., 1974; Stephan et al., 1988; Rehkämper et al., 1991; Rehkämper and Zilles, 1991].

To test the hypothesis that the tool use and considerable cognitive skills of NC crows are detectable in the size of associative forebrain components, we compared the allometric indices for the NC crow to: (1) the pooled data for the three other passerine species (European jays, sparrows and carrion crows), and (2) the carrion crow alone. We carried out the first comparison because we wished to compare the NC crow with passerines in general. The three species for which we pooled data are appropriate representatives of Passeriformes to compare with the NC crow since they all have relatively large brains [Portmann, 1947; Rehkämper et al., 1991; Boire and Baron, 1994]. The alternative of testing each species separately with NC crows was problematic because of low sample sizes for the European jay and the sparrow. We carried out the second comparison with the carrion crow to directly rule out that any enlargement of structures in the NC crow was due to an evolved characteristic of the genus *Corvus* associated with generalist foraging behavior.

We tested for differences between allometric indices using t tests. We adjusted the α level to account for multiple pair-wise t tests using the Bonferroni correction; the α level was thus set to 0.025.

Results

The brain of the NC crow has conspicuously large hemispheres (fig. 1). We provide the average body weights, brain weights and brain area volumes for the four study species in table 1. The five NC crows had significantly larger allometric indices for the mesopallium ($t = 3.917$; $p = 0.002$), striatopallidal complex ($t = 4.816$, $p < 0.001$), septum ($t = 6.940$, $p < 0.001$) and the tegmentum ($t = 3.705$, $p = 0.002$) compared to the pooled data for the three other passerines (table 2). Figures 2 and 3 give the results of the comparison for the mesopallium. The nidopallium was also larger in the NC crow, but this difference was not significant with the adjusted α level ($t =$

Table 1. Volumes of brain structures (mm^3) and body weight (g) in four Passeriformes species

	Sparrow (n = 4)	European jay (n = 2)	Carrion crow (n = 5)	NC crow (n = 5)
Brain volumes				
Total brain volume	954.88 ± 14.602	3,735.53 ± 245.713	9,573.53 ± 985.749	7,295.40 ± 741.105
Net brain volume	935.93 ± 13.391	3,647.91 ± 242.726	9,203.11 ± 1,025.258	7,227.89 ± 721.664
Hyperpallium apicale	91.08 ± 9.517	381.84 ± 6.364	963.22 ± 135.741	711.25 ± 118.957
Hyperpallium densocellulare	26.21 ± 5.274	57.88 ± 7.312	129.37 ± 25.310	78.82 ± 17.087
Mesopallium	100.05 ± 8.221	452.55 ± 9.489	1,397.41 ± 190.791	1,158.72 ± 121.010
Nidopallium	272.99 ± 21.755	1,106.21 ± 14.616	3,449.75 ± 447.439	2,546.55 ± 359.119
Entopallium	5.57 ± 1.140	27.33 ± 7.408	55.52 ± 7.695	42.38 ± 5.845
Arcopallium	31.48 ± 3.775	110.35 ± 4.299	266.15 ± 26.186	179.05 ± 17.703
Striatopallidal complex	97.31 ± 6.415	365.27 ± 53.217	848.23 ± 77.184	768.92 ± 60.682
Hippocampus	8.55 ± 1.025	25.74 ± 2.100	26.51 ± 7.845	29.20 ± 10.846
Septum	4.03 ± 0.130	17.12 ± 1.711	29.32 ± 3.478	42.50 ± 3.341
Bulbus olfactorius	0.48 ± 0.064	1.04 ± 0.368	2.01 ± 0.372	1.43 ± 0.382
Telencephalon	637.75 ± 28.607	2,545.26 ± 70.923	7,167.48 ± 864.597	5,558.55 ± 664.442
Diencephalon	44.93 ± 0.747	180.09 ± 32.089	283.52 ± 32.773	205.51 ± 32.683
Tractus opticus	13.25 ± 2.229	63.06 ± 22.691	126.04 ± 28.982	77.64 ± 4.442
Tectum	62.68 ± 1.142	244.67 ± 28.157	356.94 ± 49.750	303.79 ± 24.484
Tegmentum	84.42 ± 5.430	283.32 ± 50.685	500.95 ± 63.375	489.68 ± 17.613
Cerebellum	92.90 ± 10.58	331.51 ± 38.191	768.17 ± 94.855	592.74 ± 35.86
Body weight, g	27.18 ± 2.635	139.67 ± 16.447	466.73 ± 71.082	277.25 ± 29.874

Values are means ± SD.

Table 2. Allometric brain volume indices in four Passeriformes species

	S+J+C (n = 11)	Carrion crow (n = 5)	NC crow (n = 5)
Total brain volume (a = 0.822, b = 1.816)	0.96 ± 0.112	1.01 ± 0.157	1.10 ± 0.159
Net brain volume (a = 0.818, b = 1.814)	0.96 ± 0.107	0.94 ± 0.147	1.12 ± 0.161
Hyperpallium apicale (a = 0.838, b = 0.771)	0.98 ± 0.133	0.95 ± 0.133	1.09 ± 0.199
Hyperpallium densocellulare (a = 0.529, b = 0.647)	1.07 ± 0.204	1.14 ± 0.223	0.92 ± 0.249
Mesopallium (a = 0.959, b = 0.64)	0.92 ± 0.108*	0.88 ± 0.026*	1.22 ± 0.198
Nidopallium (a = 0.908, b = 1.141)	0.96 ± 0.103	0.94 ± 0.03	1.13 ± 0.217
Entopallium (a = 0.826, b = –0.42)	0.99 ± 0.170	0.92 ± 0.162	1.07 ± 0.127
Arcopallium (a = 0.748, b = 0.428)	1.01 ± 0.085	1.01 ± 0.098	0.99 ± 0.114
Striatopallidal complex (a = 0.794, b = 0.869)	0.93 ± 0.087*	0.88 ± 0.113*	1.20 ± 0.144
Hippocampus (a = 0.408, b = 0.394)	0.98 ± 0.270	0.87 ± 0.234	1.21 ± 0.503
Septum (a = 0.775, b = –0.45)	0.84 ± 0.174*	0.72 ± 0.170*	1.55 ± 0.220
Bulbus olfactorius (a = 0.482, b = –1.013)	1.04 ± 0.204	1.08 ± 0.233	0.98 ± 0.295
Telencephalon (a = 0.876, b = 1.574)	0.95 ± 0.114	0.94 ± 0.137	1.14 ± 0.189
Diencephalon (a = 0.635, b = 0.771)	1.03 ± 0.194	0.98 ± 0.183	0.99 ± 0.189
Tractus opticus (a = 0.769, b = 0.039)	1.06 ± 0.284	1.05 ± 0.357	0.95 ± 0.124
Tectum (a = 0.616, b = 0.951)	0.99 ± 0.205	0.92 ± 0.204	1.07 ± 0.110
Tegmentum (a = 0.655, b = 1.015)	0.94 ± 0.143*	0.88 ± 0.183*	1.19 ± 0.083
Cerebellum (a = 0.754, b = 0.898)	0.97 ± 0.128	0.96 ± 0.196	1.08 ± 0.060

Values are means ± SD. S = Sparrow; J = European jay; C = European carrion crow; a = slope of the regression line; b = intersection with the y-axis. Asterisks indicate significant differences versus NC crows.

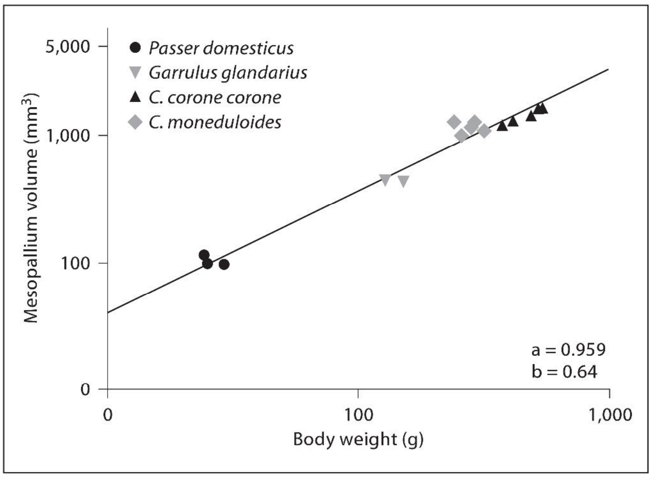

Fig. 2. Double logarithmic plot of mesopallium volume versus body weight for 16 individuals from four Passeriformes species. a = 0.959; b = 0.64.

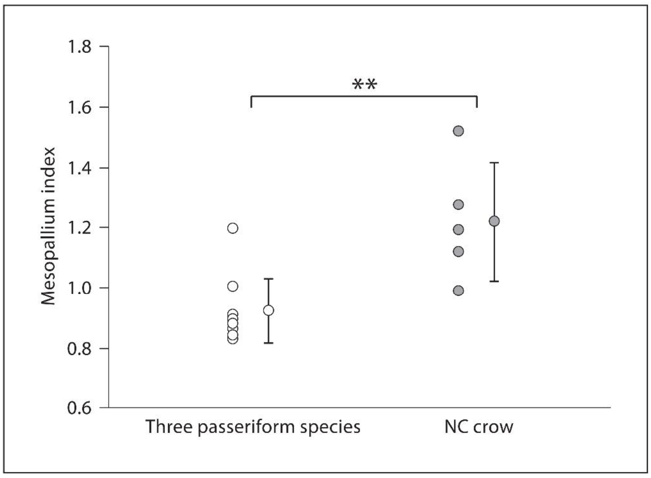

Fig. 3. Mesopallium indices for 11 individuals from three Passeriformes species *(Passer domesticus, Garrulus glandarius* and *C. corone corone)* compared to the indices for 5 NC crows. Individual data with means ± SD; ** p = 0.002. The error bars are offset from the data points for clarity.

2.174, p = 0.047). The comparison with the carrion crow *(C. corone corone)* also revealed significantly larger mean indices for NC crows in the above four structures (mesopallium: t = 3.742, p = 0.006; striatopallidal complex: t = –3.933, p = 0.004; septum: t = –6.027, $p < 0.001$, and tegmentum: t = –3.504, p = 0.008).

Discussion

Brain Structures

We found that four brain areas in NC crows are enlarged compared to the three other passerine species: mesopallium, pallidostriatal complex, septum and tegmentum. This finding supports our hypothesis that NC crows' impressive tool and general problem-solving skills are associated with enlargement of associative and motor-related structures in the forebrain.

In the following we discuss this enlargement with respect to adaptive increases of brain component size ('encephalization'). Theoretically, the enlargement that we found could also be due to adaptive decrease in body size without a corresponding decrease in brain size ('somatization'). The latter can occur in secondary dwarfism, e.g. in talapoin monkeys *Miopithecus talapoin* [Stephan et al., 1988]. Somatization can also occur through an adaptive increase in body size [Towe and Mann, 1995]. Towe and Mann investigated two populations of Botta's pocket gopher *(Thomomys bottae)*, which had adapted to habitats with different food supply, and observed a selection towards larger body sizes only. While it is possible, we think it is unlikely that somatization has occurred in any of our four study species.

The mesopallium of NC crows is significantly larger than that of the three other passeriformes we studied. This finding is consistent with previous work showing that mesopallial size predicts innovative and flexible behavior generally in birds [Timmermanns et al., 2000; Lefebvre et al., 2002, 2004]. The mesopallium as a whole is a true associative forebrain area that is not reached by any direct sensory pathway. Its ventral part includes critical areas for vocalization learning in songbirds, parrots and hummingbirds [Jarvis and Mello, 2000]. Partly overlapping with these, the anteroventral mesopallium contains a critical area for fast multimodal associative learning in the context of imprinting and avoidance learning [Rose, 2000; Horn, 2004]. A recent theory suggests that the mesopallium is also part of a circuit that controls sequencing and learning of motor actions [Feenders et al., 2008]. Thus, the mesopallium is involved in diverse associative functions and the production of learned complex motor sequences. The relative growth of this structure in NC crows makes it likely that the mental processes associated with the ability to manufacture and use tools are coupled with demands on multimodal forebrain systems.

NC crows had higher striatopallidal volumes than the other three passeriform species. Different pallial entities project into the avian striatum in a manner that parallels the mammalian brain, particularly neopallial regions such as the isocortex; for the comparability of avian and mammalian brain areas we refer to Kuhlenbeck [1967–1978], Rehkämper and Zilles [1991]; Rehkämper [1997]; Nieuwenhuys et al. [1998] and Reiner et al. [2004]. From here direct and indirect paths are sent back as loops to the pallium via a pallidothalamic pathway [Reiner, 2002]. This system was previously thought to be a mere motor pathway in primates, but is now known to primarily subserve action selection in the scope of various cognitive functions like categorization [Ashby et al., 2007], habit learning [Wickens et al., 2007] and context acquisition [Seger, 2008]. Cortical and striatal neurons form tight loops that change their firing rates in a correlated manner during the acquisition of various sensorimotor learning tasks [Brasted and Wise, 2004]. To enable these learning-related changes in firing patterns, the projection of the ascending dopaminergic system is essential, which delivers a fast feedback about the outcome of an animal's own executed behavior. The organization of the dopaminergic projection into the striatopallidal and the pallial system is highly similar in mammals and birds [Durstewitz et al., 1999], and the striatopallidal complex is equivalent to that of the mammalian brain [Reiner et al., 2004]. These similarities between birds and mammals makes it likely that the relative increase of this complex in NC crows is associated with the cognitive and motor abilities of these birds to manufacture and apply tools to various known and novel problems.

The nidopallium of NC crows is enlarged as well, but this difference is not significant. However, the enlargement is consistent with the previously reported larger nidopallium size in true tool users [Timmermanns et al., 2000]. Particularly with its associative caudolateral part (neostriatum caudolaterale), which is thought to be a functional equivalent of the mammalian prefrontal cortex [Divac and Mogenson, 1985; Güntürkün, 2005], a relative increase of nidopallium volume suggests that this structure is part of the neural machinery required for cognitive skills associated with tool use. That the mesopallium rather than the nidopallium was significantly enlarged invites obvious speculation as to the contribution of these structures to tool skills. That is, the nidopallium may have more to do with the cognitive and motor skills required for basic tool use, while an enlarged mesopallium may be required for the enhancement of basic tool skills.

The relative increase of the tegmentum and the septum is interesting. The tegmentum bears structures that serve motor control [Nieuwenhuys et al., 1998] and therefore may be involved in the fine motor skills necessary for NC crows' tool manufacture and use. However, the tegmentum is not exclusively somatomotoric but also has many sensory nuclei and vegetative control centers [Nieuwenhuys et al., 1998].

The septum may integrate a variety of stimuli for the purpose of modulating complex behavior in a temporally, spatially and socially appropriate manner, probably in cooperation with the hippocampus [Goodson et al., 2004]. However, it also has non-associative functions and the fact that the NC crow's hippocampus is not enlarged might indicate that the septal enlargement is not linked to tool use and related cognitive behavior. Thus, the heuristic value of the coincidence of the increase of these structures with observed superior cognitive skills in NC crows is limited.

The comparison of the NC crow with carrion crow indicates that the enlargement of the associative areas that we found is not due to an evolved characteristic of the genus *Corvus* associated with highly flexible generalist foraging behavior.

Tool Manufacture and the Evolution of Cognition

Tool use per se is not an indicator of cognitive ability as a wide range of animals, including invertebrates, are reported to display tool use [Beck, 1980; Hansell, 2007]. However, the underlying mechanisms responsible for the evolution of a tool using lifestyle are probably very different across animals [van Lawick-Goodall, 1970]. Evidence suggests that the mechanisms in primates and birds are closely associated with cognitive flexibility [Timmermanns et al., 2000; Lefebvre et al., 2002; Reader and Laland, 2002; Emery and Clayton, 2004; Lefebvre et al., 2004; Hunt, 2005], while those in animal groups like invertebrates are rather rigid non-cognitive ones like those for construction behavior generally in these species [Hansell, 2005, 2007]. Although NC crows do not always attend to the functional properties of the tools that they routinely use [Holzhaider et al., 2008], they use causal knowledge rather than associative learning to solve complex physical problems [Taylor et al., 2007, 2009], individually specialize for certain tools [Hunt and Gray, 2007] and have at least a rudimentary grasp of the physical properties of the objects they work on [Weir et al., 2002]. These observations indicate that tool manufacture and use in NC crows is not part of a rigid motor program, but comes from a flexible cognitive ability that makes these birds the most proficient non-human tool manufacturers. The increase of associative motor-learning-related areas that we found probably constitutes the neural basis for this cognitive ability. This finding conflicts with the recent suggestion that tool behavior in non-humans does not require special cognition but is rare simply because it is seldom useful [Hansell and Ruxton, 2008].

Our findings on the sizes of brain structures in NC crows support the hypothesis of a similar evolution of avian and mammalian brains [Karten, 1969; Rehkämper et al., 1991; Emery and Clayton, 2004; Güntürkün, 2005]. We found that the mesopallium (a true associative pallial area) as well as the striatopallidal complex are relatively enlarged in NC crows. This is also the case for primates that display proportionally enlarged associative forebrain areas and striatal volumes compared to other mammals [Stephan et al., 1988; Rehkämper et al., 1991; Keverne et al., 1996; Barton and Harvey, 2000; Sol et al., 2008]. Indeed, Stephan et al. [1988] was among the first to argue that the enlargement of the isocortex seen in apes and man is not due to primary regions like visual, auditory or somatosensory cortices, but to the non-primary areas including the association cortex.

The evolution of corvid and primate cognition and brain size has not been built on a similar evolution of the detailed architecture of their forebrains. While mammals have a laminar arrangement of their pallium thus forming a cortex, the avian pallium displays a nuclear arrangement with a layering restricted to relatively small areas [Rehkämper et al., 1984; Ebinger et al., 1992; Jarvis et al., 2005]. Thus, cognition in corvids and primates evolved similarly with respect to mental capabilities, despite building on a different system of microcircuits [Güntürkün, 2005]. Our data, then, reveal an important additional principle of the evolution of cognitive functions: despite a different internal microstructure, an evolutionary increase of cognitive skills goes along with a volume increase of associative forebrain structures [Rehkämper et al., 1991]. In other words, enlargement of associative forebrain structures seems to be the default option in the evolution of cognitive skills.

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Mosaic Evolution and Adaptive Brain Component Alteration under Domestication Seen on the Background of Evolutionary Theory

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Key Words
Domestication · Pigeons · Brain component size · Hippocampus · Olfactory bulb · Adaptation · Evolution

Abstract

Brain sizes and brain component sizes of five domesticated pigeon breeds including homing (racing) pigeons are compared with rock doves *(Columba livia)* based on an allometric approach to test the influence of domestication on brain and brain component size. Net brain volume, the volumes of cerebellum and telencephalon as a whole are significantly smaller in almost all domestic pigeons. Inside the telencephalon, mesopallium, nidopallium (+ entopallium + arcopallium) and septum are smaller as well. The hippocampus is significantly larger, particularly in homing pigeons. This finding is in contrast to the predictions of the 'regression hypothesis' of brain alteration under domestication. Among the domestic pigeons homing pigeons have significantly larger olfactory bulbs. These data are interpreted as representing a functional adaptation to homing that is based on spatial cognition and sensory integration. We argue that domestication as seen in domestic pigeons is not principally different from evolution in the wild, but represents a heuristic model to understand the evolutionary process in terms of adaptation and optimization.

This paper is dedicated to the late John Maynard Smith and his lifelong effort to understand evolution as an adaptive optimization process.

Introduction

The history of domestication has been described in many publications mostly based on zooarchaeological data or on documents such as writings, coins, ornamented pottery or similar items [Zeuner, 1963; Clutton-Brock, 1981; Mason, 1984; Crawford, 1990; Benecke, 1994]. Another approach has been to compare wild living species with domesticated animals both thought to originate from a common ancestor. This has been done for some birds [Sossinka, 1982] and many mammalian species. In Germany, Herre and Röhrs [1971] have formulated a research strategy that has guided the work of many others [see Kruska, 1988]. Between the lines these authors and others regard domesticated animals as 'victims' that have undergone regressive evolution. This is obvious in the work of Hemmer [1990] who claims a 'decline of environmental appreciation' for domesticated animals. Here we will refer to this point of view regarding domesticated animals as the 'regression hypothesis'.

Empirical data on brain sizes seem to support this point of view. In dogs (poodles), for example, brains were

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29.8% smaller than in wolves [Weidemann, 1970; Ebinger, 1980], and Zimen [1971] registered behavioral deficits in dogs compared to wolves. In ducks, Ebinger [1995] also found brain size reduction, and he speculated that this might be correlated with a reduction in dabbling behavior of domestic ducks because dabbling requires an elaborate somatosensory system and corresponding nuclei in the brain.

The term 'regressive' includes a negative connotation that seems inappropriate to us. If we accept that 'evolutionary progress' [see Ruse, 1996] is accompanied by (1) an increasing fitness defined as an increasing number of offspring [Haldane, 1932; Thoday, 1953] and (2) a geographic spreading as a consequence of optimization [Maynard Smith, 1982; Gomulkiewicz, 1998], then 'evolutionary regressions' would mean the opposite. However, it is a fact that domestic animals are evolutionarily extremely progressive because their reproductive rates can be enormous and they occupy much more terrain than their wild ancestors ever had. This can be seen in dogs, sheep, goats, cattle and particularly in poultry and pigeons.

The 14 extant rock dove subspecies *(Columba livia ssp.)* [Howard and Moore, 1991] that represent the gene pool from which domestic pigeons are derived still inhabit the original terrain around the Mediterranean Sea and adjacent areas [see Hawes, 1984, or Johnston and Janiga, 1995, for short review and further literature]. Domestic pigeons, however, are found worldwide. Using homing (racing) pigeons and four fancy pigeon breeds we tested the hypothesis that domestic animals are successfully adapted to an ecological niche defined by man. This adaptation is accompanied by peculiarities in brain structure and brain composition. It is the purpose of this paper to demonstrate that such adaptation includes not only size decreases but also increases in the sizes of brain components associated with the functions selected for by human intervention.

Materials and Methods

The brains of 10 (5 male, 5 female) rock doves *(Columba l. livia)*, 10 homing (racing) pigeons (5 male, 5 female) and 39 fancy pigeons were investigated (fig. 1). The rock dove brains originate from a sample collected in Turkey and were described in earlier papers on organ weights in wild and domestic pigeons [Löhmer and Ebinger, 1980; Ebinger and Löhmer, 1984]. The homing pigeons were raised in the loft of a successful breeder and we acquired them while they were alive.

Of more than 250 fancy pigeon breeds we have chosen individuals from four breeds: 9 (4 male, 5 female) figurita frills (Valencian frill, Valencian figurita) because of their small size, 10 oriental roller (5 male, 5 female) because of their ability to fly high and wide, 10 Saxonian croppers (7 male, 3 female) because they represent a type very different from the wild form and 10 King (6 male, 4 female) because of their large size. It should be noted that sex determination based on appearance is difficult and thus was done during dissection (see below). Individuals of these fancy breeds were delivered live by successful breeders. All animals used in this study were adults.

After their body weights were determined, the individuals were sacrificed by an overdose of anaesthesia and subsequently perfused with saline solution and a fixative (Bodian's solution) via the left ventricle. Via inspection of the intestine we ascertained that the individuals had not been fattened or had signs of nutrient supplements. Brains were removed, weighed and embedded in paraffin. The brain weight was taken immediately (<60 min) after perfusion [fresh brain weight; Wree, 1986]. All brains were serially sectioned (20 μm) in a coronal plane. Every 5th section was mounted and stained for perikarya using a silver technique [Gallyas, 1971].

On at least 50 sections distributed at equal distances from rostral to caudal the area of brain tissue was measured using computer-controlled planimeter equipment, and the volume of the total brain was calculated. Due to shrinkage, which might be different from brain to brain even if the brains have been treated equally [Stephan et al., 1981], the volume based on serial sections is smaller than the fresh volume. A correction factor was calculated for each individual brain as a quotient of fresh brain volume/embedded brain volume. This factor was used to correct all the measured volumetric brain component data and to convert them to fresh volumes in an individual brain. This shrinkage factor lies between 40.5% and 48.8% in Bodian-perfused and paraffin-embedded material.

Six fundamental brain components, brain stem, cerebellum, optic tectum, optic tract, diencephalon, and telencephalon were measured. In the case of optic tract and tectum, the data have been summed for this investigation because there is a close functional relationship with the optic tract fibers mainly reaching the upper layers of the optic tectum. After measuring the fundamental brain components seven telencephalic components were investigated. According to the new nomenclature [Reiner et al., 2004] these are (traditional nomenclature in parentheses): (1) hyperpallium apicale + densocellulare, shortly hyperpallium apicale+ (hyperstriatum accessorium + dorsale); (2) mesopallium (hyperstriatum ventrale); (3) nidopallilum + entopallium + arcopallium, shortly nidopallium+ (neostriatum + ectostriatum and archistriatum); (4) striatum laterale + globus pallidus + striatum mediale + tuberculum olfactorium, shortly striatum laterale+ (paleostriatum + lobus parolfactorius + tuberculum olfactorium); (5) hippocampus; (6) septum; and (7) bulbus olfactorius. Figure 2 illustrates some of these areas. A definition of the borderlines of these areas is given by Rehkämper et al. [1991a]. Care was taken that every brain component of interest was visible on at least 6 sections so that volume determination has an error less than 5% [Zilles et al., 1982; Gundersen and Jensen, 1987]. Based on these data the net brain volume was calculated as the sum of the single brain components. In contrast to brain volume, the net brain volume does not include the volume of leptomeninges, ventricles, choroid plexus and remains of brain nerves.

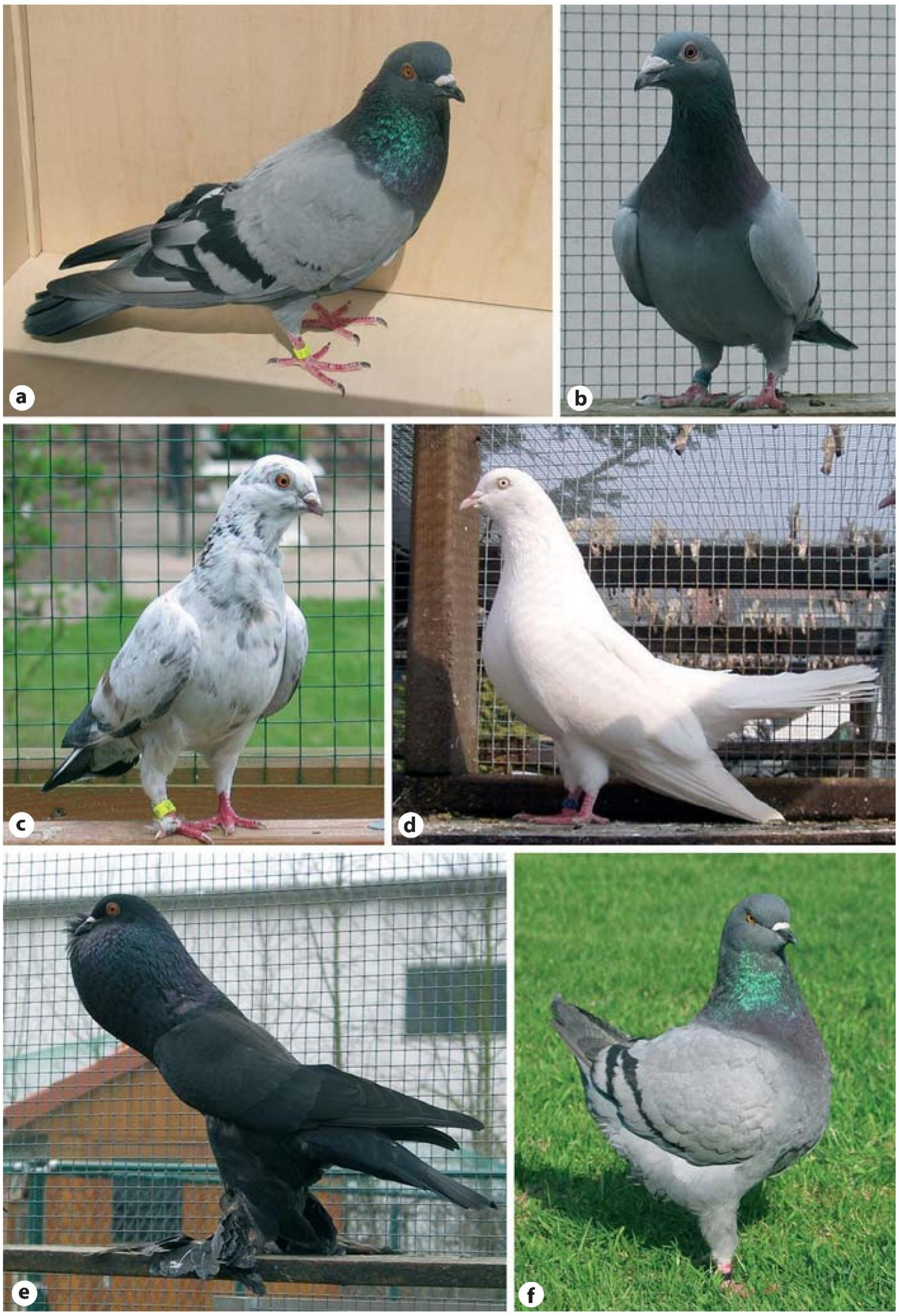

Fig. 1. Pigeons investigated: **a** Rock Dove, **b** Homing (Racing) Pigeon, **c** Figurita Frill, **d** Oriental Roller, **e** Saxonian Cropper; **f** King (not to scale).

The difference in body size between rock doves, homing pigeons and fancy pigeons makes an allometric approach necessary if brain (or brain component) sizes are to be compared [Snell, 1892; Dubois, 1897; Harvey, 1988; Mann et al., 1988; Stephan et al., 1988]. This method includes the calculation of a regression line slope that expresses the brain (or brain component) size/body size relationship. To obtain accurate, reliable slopes, data should originate from a sample that covers a reasonable body weight range and whose individual members are part of a biologically significant group, for example a taxonomic unit. The former is not given in case of single breeds, however, both criteria are met given the inclusion of all 59 individuals investigated. There is a reasonable body weight range and all individuals belong to breeds which are subgroups of the taxon *Columba livia*.

A Pearson correlation test was calculated to ascertain whether there is a significant correlation between brain (component) size and body weight and thus if an allometric approach is needed. If the correlation is not significant fresh volumes are compared directly across breeds.

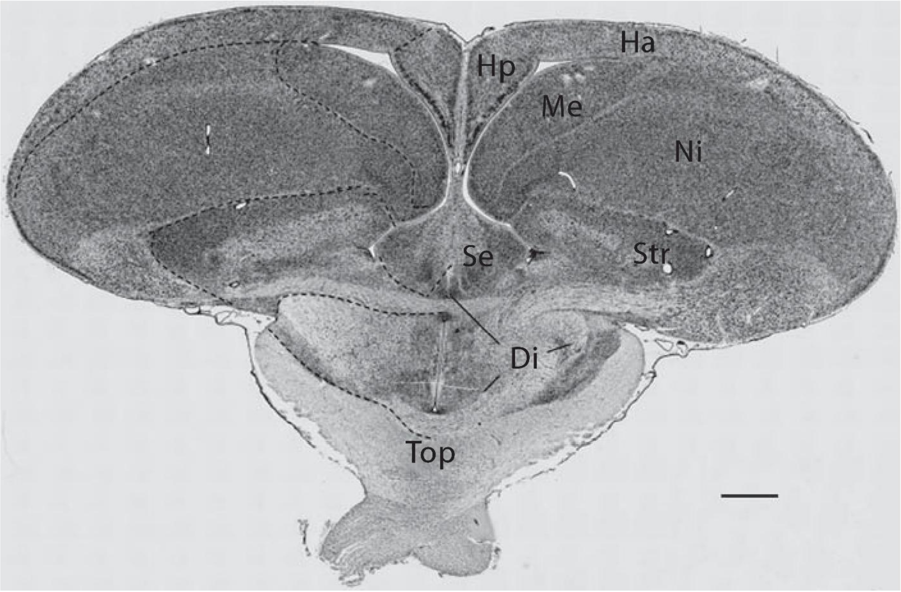

Fig. 2. Coronal section through the brain of a Homing Pigeon to illustrate some subdivisions. (Di diencephalon, Hp hippocampus, Ha hyperpallium apicale+, Me mesopallium, Ni nidopallium+, Str striatum laterale+, Se septum, Top tractus opticus). Gallyas stain, scale 1 mm.

Table 1. Body weight (g), net brain size and fundamental brain components

Breed	BoW	Net vol	Tegm	Cere	Tectum	Top	Di	Tel
Rock Dove (n = 10)	298.99 (±37.85)	2,086.11 (±96.12)	302.42 (±21.62)	336.44 (±28.56)	218.02 (±12.80)	50.93 (±3.67)	133.43 (±8.12)	1,044.87 (±45.62)
Homing Pigeon (n = 10)	462.78 (±34.63)	2,299.71 (±101.65)	356.80 (±32.80)	360.07 (±20.57)	223.36 (±9.77)	88.54 (±9.41)	145.48 (±8.64)	1,125.46 (±59.93)
Figurita Frill (n = 9)	220.44 (±19.15)	1,720.18 (±75.56)	251.93 (±20.27)	253.39 (±20.54)	166.00 (±10.11)	51.98 (±7.86)	108.50 (±10.33)	888.39 (±39.93)
Oriental Roller (n = 10)	321.60 (±21.25)	1,952.85 (±108.90)	302.81 (±15.90)	303.20 (±29.22)	181.68 (±10.09)	60.50 (±7.10)	124.66 (±13.02)	980.00 (±84.21)
Saxonian Cropper (n = 10)	466.50 (±45.46)	2,357.19 (±102.79)	362.91 (±15.95)	383.51 (±34.12)	236.16 (±8.48)	105.22 (±16.43)	148.62 (±14.12)	1,120.77 (±65.35)
King (n = 10)	852.00 (±90.06)	2,845.70 (±117.35)	445.99 (±29.14)	436.65 (±34.20)	266.08 (±21.66)	118.53 (±16.57)	182.16 (±16.42)	1,396.29 (±65.64)

Means in mm^3, standard deviation in parentheses.

BoW = Body weight; Cere = cerebellum; Di = diencephalon; Net vol = net brain volume; Tegm = tegmentum; Tel = telencephalon; Top = tractus opticus.

If the correlation was significant, regression lines and allometric size indices (residuals) for every analyzed brain (or brain component) were calculated and compared across breeds. This allowed us to test whether the brain or a given brain component is larger or smaller in domesticated homing pigeons or fancy pigeons compared to wild rock doves independently of the different body sizes.

The slopes of brain (or brain component)/body weight relations were calculated according to the formula:

$$\log \textit{brain (or brain component) size} = \log b + a \cdot \log \textit{body size}$$

where '*a*' is the slope and '*b*' the intersection with the y axis. Residuals R were calculated according to the formula

$$R = \frac{\textit{actual brain (component) size}}{\textit{expected brain (component) size}} \cdot 100$$

Table 2. Telencephalic brain components

Breed	Ha	Me	Ni	Str	Hp	Se	Bol
Rock Dove (n = 10)	183.02 (±45.62)	178.98 (±9.58)	482.1 (±23.67)	146.36 (±10.53)	32.37 (±5.59)	13.28 (±1.24)	8.76 (±1.29)
Homing Pigeon (n = 10)	188.75 (±17.32)	179.16 (±15.72)	511.82 (±25.90)	166.83 (±11.98)	54.38 (±4.70)	15.35 (±1.38)	9.22 (±1.28)
Figurita Frill (n = 9)	142.28 (±11.51)	161.09 (±9.66)	401.93 (±23.48)	128.39 (±12.31)	36.80 (±3.50)	12.19 (±0.87)	5.72 (±0.78)
Oriental Roller (n = 10)	159.11 (±19.17)	163.09 (±17.87)	453.08 (±46.73)	138.03 (±10.28)	44.47 (±3.29)	14.98 (±1.07)	7.28 (±1.24)
Saxonian Cropper (n = 10)	177.17 (±21.08)	195.72 (±9.95)	506.28 (±40.78)	171.31 (±7.97)	45.19 (±3.36)	16.49 (±1.35)	8.71 (±0.88)
King (n = 10)	240.91 (±23.85)	236.97 (±18.54)	634.59 (±36.02)	194.76 (±14.99)	59.03 (±6.76)	22.58 (±3.36)	7.46 (±1.99)

Means in mm^3, standard deviation in parentheses.

Bol = Bulbus olfactorius; Ha = hyperpallium apicale+; Hp = hippocampus; Me = mesopallium; Ni = nidopallium+; Str = striatum laterale+; Se = septum.

Table 3. Results of the Pearson correlation test (r = Pearson correlation coefficient) for brain and brain component volume vs. body weight

Net vol	Tegm	Cere	Tc/Top	Di	Tel	
$r = 0.937$ $p < 0.001$	$r = 0.912$ $p < 0.001$	$r = 0.831$ $p < 0.001$	$r = 0.876$ $p < 0.001$	$r = 0.882$ $p < 0.001$	$r = 0.924$ $p < 0.001$	
Ha	**Me**	**Ni**	**Str**	**Hp**	**Se**	**Bol**
$r = 0.825$ $p < 0.001$	$r = 0.85$ $p < 0.001$	$r = 0.894$ $p < 0.001$	$r = 0.833$ $p < 0.001$	$r = 0.741$ $p < 0.001$	$r = 0.886$ $p < 0.001$	$r = 0.155$ $p = 0.24$

Bol = Bulbus olfactorius; Cere = cerebellum; Di = diencephalon; Ha = hyperpallium apicale+; Hp = hippocampus; Me = mesopallium; Net vol = net brain volume; Ni = nidopallium+; Se = septum; Str = striatum laterale+; Tc = tectum opticum; Tegm = tegmentum; Tel = telencephalon; Top = tractus opticus.

The expected brain (or brain component) size is the value on the regression line that corresponds to a given individual body weight.

Residuals of brain weight, net brain volume and brain component volumes were compared for rock doves and domestic pigeons and the significance of the differences were tested using Student's t test.

The original research reported herein was performed under the guidelines of the German law to prevent cruelty to animals.

Results

Average body weights, brain weights and brain component volumes in rock doves, homing pigeons and the four fancy breeds are given in tables 1 and 2 and will not be repeated here. The Pearson correlation test demonstrates a significant correlation between brain (component) size and body weight except in case of the olfactory bulb which had a very low slope of 0.155 (table 3). Thus, allometric size residuals (means and standard deviation)

Table 4. Allometric size residuals of fundamental brain components

Breed	Net Vol a = 0.355 b = 2.418	Tegm a = 0.406 b = 1.465	Cere a = 0.373 b = 1.563	Tc/Top a = 0.425 b = 1.355	Di a = 0.359 b = 1.211	Tel a = 0.314 b = 2.217
Rock Doves (n = 10)	105.58 (± 4.61)	102.66 (± 5.81)	110.01 (± 8.37)	105.63 (± 4.61)	106.31 (± 6.48)	106.12 (± 5.21)
Homing Pigeon (n = 10)	99.53 (± 4.69)** p = 0.009	101.42 (± 10.32) p = 0.743	99.90 (± 5.23)** p = 0.005	101.55 (± 5.37) p = 0.085	99.02 (± 7.37)* p = 0.031	99.49 (± 5.29)* p = 0.011
Figurita Frill (n = 9)	96.82 (± 2.65)*** p < 0.001	96.66 (± 6.97) p = 0.056	92.64 (± 5.99)*** p < 0.001	97.18 (± 5.92)** p = 0.003	96.3 (± 9.07)* p = 0.013	99.11 (± 3.7)** p = 0.004
Oriental Roller (n = 10)	96.09 (± 4.54)*** p < 0.001	99.67 (± 5.54) p = 0.254	96.27 (± 8.60)** p = 0.002	92.06 (± 6.14)*** p < 0.001	96.60 (± 10.41)* p = 0.022	96.99 (± 7.5)** p = 0.005
Saxonian Cropper (n = 10)	101.82 (± 5.78) p = 0.126	102.79 (± 4.52) p = 0.956	106.28 (± 10.99) p = 0.404	110.92 (± 7.58) p = 0.076	100.90 (± 10.45) p = 0.181	98.19 (± 5.8)** p = 0.005
King (n = 10)	99.19 (± 2.92)** p = 0.002	98.94 (± 6.80) p = 0.205	96.51 (± 7.04)*** p = 0.001	96.63 (± 7.29)** p = 0.004	99.37 (± 6.04)* p = 0.023	101.95 (± 4.20) p = 0.064

Means ± standard deviation in parentheses.

*, **, *** Significant difference (5, 1 and 0.1% level) between rock doves and domestic pigeons.

Cere = Cerebellum; Di = diencephalon; Net vol = net brain volume; Tc = tectum opticum; Tegm = tegmentum; Tel = telencephalon; Top = tractus opticus.

for brain size and brain component volumes of rock doves, homing pigeons and the four fancy breeds were calculated and are found in tables 4 and 5. The non-correlation of olfactory bulb volume and body weight allows a direct comparison of the absolute volumes (means and standard deviation, table 5, right column, table 6).

We used these data to test whether there are significant size differences between homing pigeons and single fancy pigeon breeds on the one hand and rock doves on the other.

Rock Doves versus Homing Pigeons

Net brain volume, cerebellum, diencephalon and telencephalon as a whole as well as hyperpallium apicale+, mesopallium and nidopallium+ are significantly smaller in homing pigeons. The tegmentum, optic tectum + optic tract, striatum laterale+, septum and olfactory bulb are equivalently sized in the 2 species. The hippocampus is significantly larger in homing pigeons.

Rock Doves versus Figurita Frills

Brain volume, cerebellum, optic tract + optic tectum, diencephalon, telencephalon, hyperpallium apicale+, nidopallium+, and olfactory bulb are significantly smaller in figurita frills. The tegmentum, mesopallium, striatum laterale+ and septum are equivalently sized in the 2 breeds. The hippocampus is significantly larger in figurita frills.

Rock Doves versus Oriental Roller

Net brain volume, cerebellum, optic tract + optic tectum, diencephalon, telencephalon, hyperpallium apicale+, mesopallium, nidopallium+, striatum laterale+, and olfactory bulb are significantly smaller in oriental rollers. Of equal size is the tegmentum and hippocampus and septum are significantly larger.

Rock Doves versus Saxonian Croppers

In Saxonian croppers, the telencephalon, hyperpallium apicale+, and nidopallium+ are significantly smaller. Of equal size are net brain volume, tegmentum, cerebel-

Table 5. Allometric size residuals of telencephalic brain components

Breed	Ha a = 0.342 b = 1.363	Me a = 0.278 b = 1.543	Ni a = 0.31 b = 1.887	Str a = 0.313 b = 1.379	Hp a = 0.401 b = 0.602	Se a = 0.429 b = 0.075	*Bol*
Rock Doves (n = 10)	113.25 (± 9.20)	105.31 (± 5.82)	107.12 (± 6.28)	102.91 (± 7.29)	82.41 (± 13.35)	97.09 (± 8.66)	*8.76* *(81.29)*
Homing Pigeons (n = 10)	100.38 (± 8.85)** p = 0.005	93.27 (± 8.60)** p = 0.002	99.12 (± 4.65)** p = 0.005	102.20 (± 7.85) p = 0.835	116.19 (± 10.43)*** p < 0.001	92.96 (± 8.90) p = 0.307	*9.22* *(81.28)* *p = 0.436*
Figurita Frill (n = 9)	97.57 (± 8.25)** p = 0.001	103.11 (± 7.32) p = 0.475	97.93 (± 4.41)** p = 0.002	99.08 (± 7.85) p = 0.285	105.92 (± 10.52)*** p < 0.001	101.48 (± 7.59) p = 0.259	*5.72* *(80.78)**** *p < 0.001*
Oriental Roller (n = 10)	95.77 (± 11.06)** p = 0.001	93.76 (± 9.15)** p = 0.003	98.14 (± 9.46)* p = 0.022	94.66 (± 6.04)* p = 0.013	109.94 (± 8.70)*** p < 0.001	106.00 (± 7.18)* p = 0.022	*7.28* *(81.24)** *p = 0.017*
Saxonian Cropper (n = 10)	94.02 (± 11.26)*** p < 0.001	101.72 (± 6.25) p = 0.2	97.91 (± 8.61)* p = 0.014	104.83 (± 6.68) p = 0.548	96.33 (± 7.9)* p = 0.011	99.75 (± 10.30) p = 0.54	*8.71* *(80.88)* *p = 0.917*
King (n = 10)	104.03 (± 9.76)* p = 0.043	104.10 (± 7.62) p = 0.694	101.79 (± 4.67)* p = 0.045	98.69 (± 8.68) p = 0.254	98.97 (± 12.90)* p = 0.011	105.14 (± 14.24) p = 0.144	*7.46* *(81.99)* *p = 0.098*

Means ± standard deviation in parentheses; in case of the olfactory bulb, fresh volumes were calculated instead of allometric residuals (see Material and Method and Result section).

*, **, *** Significant difference (5, 1 and 0.1% level) between rock doves and domestic pigeons.

Bol = Bulbus olfactorius, Ha = hyperpallium apicale+; Hp = hippocampus; Me = mesopallium; Ni = nidopallium+; Str = striatum laterale+; Se = septum.

Table 6. Fresh volumes of the olfactory bulb compared between homing pigeons and four other domestic pigeon breeds

Homing Pigeon	Figurita Frill	Oriental Roller	Saxonian Cropper	King
9.22 (± 1.28)	5.72 (± 0.78)*** p < 0.001	7.28 (± 1.24)** p = 0.003	8.71 (± 0.88) p = 0.312	7.46 (± 1.99)* p = 0.03

Means ± standard deviation in parentheses.

*, **, *** Significant difference (5, 1 and 0.1% level).

lum, optic tract + optic tectum, diencephalon, mesopallium, striatum laterale+, septum, and olfactory bulb. The hippocampus is significantly larger.

Rock Doves versus King

In king pigeons net brain volume, cerebellum, optic tract + optic tectum, diencephalon, hyperpallium+ and nidopallium+ are significantly smaller than in Rock Doves. Of equal size are tegmentum, telencephalon, mesopallium, striatum laterale+, septum and olfactory bulb. The hippocampus is significantly larger.

The Position of Homing Pigeons in Comparison to the Domestic Fancy Pigeons

Among the domestic pigeons investigated, homing pigeons are special because they are selected for a well defined, quantifiable trait: returning to the home loft from distant release sites as quickly as possible. This was the

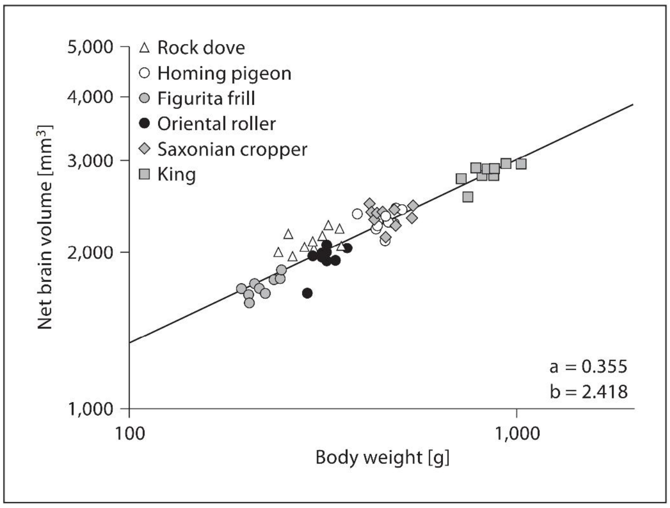

Fig. 3. Net brain volume (mm^3) of rock doves and five domestic pigeon breeds in relation to body weight (g). Allometric size residuals are given in table 4.

rationale for comparing homing pigeons with the four other domesticated breeds. Most interesting is the finding that in comparison to the four fancy breeds the average index of the homing pigeons' olfactory bulb is largest and this difference is significant with respect to figurita frills, oriental roller and king (table 6). Only in case of the Saxonian Croppers did this difference not reach significance.

Discussion

Net Brain Volume

It was found that in general the net brain volume of domesticated pigeons (homing pigeons and fancy breeds) is smaller when compared to the wild rock dove (fig. 3). This seems to support the interpretation that there is a regression in brain size under domestication and it is in agreement with Löhmer and Ebinger [1980] and Ebinger and Löhmer [1984]. However, a closer look makes it clear that the story is somewhat more complicated because an overall decrease masks the fact that single brain components of domestic pigeons are as large or even larger than in the wild form.

One fancy breed, the Saxonian cropper, is not reduced in brain size which is not easy to interpret. Saxonian croppers are by no means 'half-wild' or less domesticated than other breeds. The upright position, the large crop and feathery legs and feet (fig. 1) are clear indications of domestication that are not seen in wild rock doves and even seldom found in feral pigeons [Johnston and Janiga, 1995]. It is unlikely that Saxonian croppers can live outside a man-made environment and this underlines their status as domesticated animals. In body weight they are close to homing pigeons (table 1). Thus, absolute data on brain volume and brain component volumes can be compared which we have done in this discussion chapter. The volumes of net brain, tegmentum, cerebellum and telencephalon as a whole are not different. Significantly larger are optical tract/tectum, and mesopallium, and significantly smaller is the hippocampus (these findings are the same if allometric indices are compared). Thus, although the size of the brain is similar, brain composition is different between the two breeds. To date, Saxonian croppers have not been the subject of scientific investigation although it might be worthwhile to study Saxonian croppers more intensively, particularly in respect to their neurobiology.

Tegmentum

The tegmentum is as large in the homing pigeons and all four fancy breeds as it is in the wild rock doves. Thus there is no size alteration under domestication. This obviously is in analogy to brain evolution in mammals and supports the hypothesis of parallel evolution in birds and mammals [Rehkämper and Zilles, 1991; Emery and Clayton, 2004]. Stephan and co-workers [for review see Stephan et al., 1991] have drawn attention to evidence that the tegmentum contains centers of vegetative function and therefore might be regarded as a brain component for basic biological needs that cannot be reduced. This conservation of the size of nervous structures also lies behind the calculations of indices by Portmann indicating progression of encephalization [Portmann, 1946, 1947] and in a way also behind Jerison's theory of extra neurons, which regards the brain stem as conservative [Jerison, 1973]. Single wild mammalian species (semiaquatic insectivores) show comparatively enlarged tegmenta because of sensory specialization [trigeminal system; Stephan and Bauchot, 1959; Stephan and Spatz, 1962; Stephan and Kuhn, 1982] and the same is seen in water fowl [Dubbeldam, 1994; Ebinger, 1995]. However, in general the tegmentum has limited evolutionary capacity for volume alteration across species.

Cerebellum

The cerebellum is relatively reduced in the domesticated pigeons. We know from mammals [bats; Baron et al., 1996] and from some birds [humming birds; Rehkämper et al., 1991b; crows, parrots, woodpeckers; Sultan, 2005] that elaborated cerebella are associated with a high degree of maneuverability during flight. Rock doves, which live in rocky landscapes and need to escape from predators such as peregrines, might profit from such behavior. However, none of the domestic pigeons have been bred for solving problems like that. Even homing pigeons, which are excellent flyers, are selected for quickness and perseverance in flight, but not for maneuverability.

Tectum/Optic Tract

Except in homing pigeons (and Saxonian croppers) this part of the visual system is reduced in domesticated pigeons. Visually guided behavior is well studied in homing pigeons. For example, cognitive tasks (mental rotation, match to sample) that are based on visual integration can be performed extremely quickly [Hollard and Delius, 1982; Lissek and Güntürkün, 2004] and recently it has been shown that high flying homing pigeons make use of visual cues such as motorways to find their way home [Lipp et al., 2004]. Such performances depend on the structure of the eye and its retina as well as on cognitive abilities, which might be associated with deeper layers of the tectum that are known to be integrative [see Dubbeldam, 1994]. To date, there are no investigations that compare the structure of the visual system and its subsystems and related behavior across breeds. Thus related questions remain unanswered.

Diencephalon

The diencephalon shows a decrease in volume when homing pigeons and fancy breeds are compared to wild rock doves. This brain component is integrated into visual [Güntürkün, 1991], auditory [Karten, 1968] and motor systems and includes hypothalamic areas [for review see Dubbeldam, 1994]. Additionally, the cerebellum projects to the diencephalon [via the rostral peduncle; Arends and Zeigler, 1991]. Thus its size reduction probably mirrors alterations in these systems and thus partially reflects size alterations seen on the telencephalic or cerebellar level.

Telencephalon and Its Components, Particularly Hippocampus and Olfactory Bulb

The telencephalon as a whole seems to be reduced in size in all domestic pigeons, which correlates with the overall brain size reduction. However, there is one telencephalic component, the hippocampus, that does not follow the trend and is significantly larger in all domesticated breeds when compared with the wild form. This is the first documented brain component that is enlarged under the constraints of domestication compared to the wild form. Clearly this observation does not fit the regression hypothesis. On the contrary we understand it as a progressive functional adaptation to the man made environment.

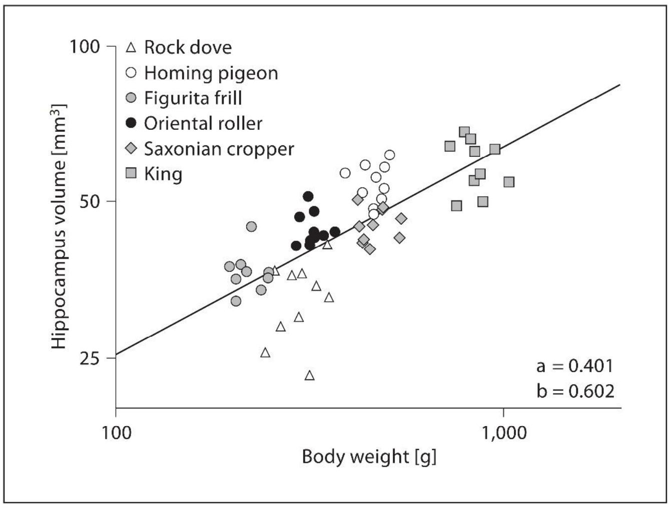

Fig. 4. Hippocampus volume (mm^3) of rock doves and five domestic pigeon breeds in relation to body weight (g). Allometric size residuals are given in table 5.

As can be seen in figure 4, the hippocampi of most individuals of figurita frills (mean residual 105.9), oriental rollers (mean residual 109.9) and particularly homing pigeons (mean residual 116.2) are above the reference line. These three groups are more or less characterized by their flying abilities. Many of the ‘roller’ pigeon breeds can fly very high and far and still return safely to their loft. Unfortunately, there is no scientific publication that explicates the breed history of homing pigeons. However, popular reports agree that roller pigeons stand at the beginning of the breeding of the modern homing pigeons. The same is true for domestic pigeons of the frill group [Levi, 1965; Rösler, 1982].

The creation of the homing (racing) pigeon started in Belgium at the beginning of the 19th century [Levi, 1965; Rösler, 1982]. Pigeon races were used to select for individuals demonstrating a quick and reliable return to the home loft. Thus, ‘homing’ is the important operating term. It is well proven that the homing ability of modern homing pigeons is superior to that of wild rock doves. Alleva et al. [1975] and Visalberghi et al. [1978] have compared the homing ability of rock doves with homing pigeons. The performance of rock doves was much poorer than that of homing pigeons, particularly if covering longer distances is required. In their analyses, comparatively more rock doves were lost or reached their home loft late, some individuals not before several days.

The ethological and neuronal basis of homing has been investigated intensively [for review see Wallraff, 2005]. Lipp [1996] has pointed out that homing in homing pigeons is based on multimodal sensory integration, motivation and experience. Among the sensory systems, vision and magnetic sensitivity are doubtlessly involved. Papi has drawn attention to the role of olfaction [Papi et al., 1974]. After strong disputes there is a general agreement that olfactory cues can influence homing behavior. This receives additional neural support in the form of the relatively large olfactory bulbs as described here and in a former study [Rehkämper et al., 1988].

The multimodal integration of homing is based on spatial cognition [Wallraff, 2005]. This has its structural base in the hippocampus. In wild mammalian and avian species it has been demonstrated that food storing species, which are challenged in spatial cognition, have relatively large hippocampi [Sherry et al., 1989; Clayton and Krebs, 1994; Jacobs, 1995; Healy and Krebs, 1996; Bingman et al., 2003, 2005]. Standing out among mammals are elephant shrews with extraordinary large and well developed hippocampi [Stephan et al., 1991; Rehkämper, 1981; Rehkämper et al., 1995]. This can be correlated with superior spatial cognition because in large home ranges many sheltering places are remembered and found extremely quickly by the elephant shrews if necessary [Sauer, 1973]. In many papers Bingman and collaborators have shown that homing in homing pigeons depends very much on hippocampus function [Bingman et al., 2003, 2005]. Thus, what characterizes the brain of homing pigeons (and related breeds) can be understood as an adaptation to homing.

Size alteration of the olfactory bulb is in parallel with that of the hippocampus. In an earlier publication we reported that the olfactory bulb of homing pigeons is larger than that in non-homing breeds [Rehkämper et al., 1988]. This finding is further supported in the present study. The olfactory bulb of homing pigeons is significantly larger than that in figurita frills, oriental rollers and kings (table 6). As previously mentioned, olfaction is part of the homing ability and thus these data support the idea of the homing pigeon as strongly adapted to perform this behavior. A more detailed discussion can be found in Rehkämper et al. [1988, 1995, 2001].

In mammals, the olfactory system might be the only sensory system that projects directly into the precommisural hippocampus [Stephan, 1975]. Reiner and Karten [1985] investigated olfactory bulb projections in the pigeon and found connections from the olfactory bulb to the rostromedial forebrain. In geese we have shown that there is also a projection of the olfactory bulbs to the rostromedial telencephalon [Ebinger et al., 1992] and this is very strong. The labeled area is in continuation with the caudomedial parts of the hyperpallium apicale including an analog to the entorhinal region of mammals, which in this vertebrate class gives origin to the perforant tract that reaches the fascia dentata of the hippocampus proper. We therefore propose the idea that under certain circumstances the development of the olfactory system and the development of the hippocampus might occur in parallel, at least in part. Again, more detailed analyses are needed for proof.

Some Remarks with Respect to Evolutionary Theory

It can be seen that the brain of domesticated pigeons in general is allometrically smaller than that of wild rock doves, but single brain components have undergone no decrease or are even larger. This is an example of mosaic evolution [Simpson, 1959; Mayr, 1963] which means that subsystems of the brain might follow different trends of (size) alteration independently from others. Recently, such mosaic evolution has been demonstrated under diverse evolutionary pressures for the brain of wild mammals [Barton and Harvey, 2000]. Clark et al. [2001] showed mosaic evolution in the case of the cerebellum of bats and whales. Similar principles were described for wild avian species that belong to different 'cerebrotypes' [Iwaniuk and Hurd, 2005; see also Iwaniuk et al., 2004].

Seeing mosaic evolution in the wild and under domestication strengthens our point of view that domestication can serve as a generalized model of evolution, particularly with respect to the problem of selection and evolution. This is not a new problem. (We would like to mention the name of Sewal Green Wright who has contributed substantially to debates on the role of selection for evolution. A biography as well as a compilation of his papers are available [Provine 1986a, b].)

We see, in principle, no difference between organismal plasticity in the wild and under laboratory or domestic conditions. The so called 'artificial selection' under domestication and the so called 'directional selection' in the wild can be treated in the same way [see Rice, 2004]. The fact that changes under domestication can occur very quickly, which means in a few generations, is no problem, particularly with respect to brain evolution because it has been shown that brain size can change very fast, even in the wild [Kruska, 1987].

In the wild, the criteria of selection are often difficult to ascertain because the parameters that characterize an ecological niche might be manifold and not easily accessible to analysis, and there is less chance for an experimental approach. However, if we draw parallels between selected criteria resulting from the breeding requirements of humans with selective criteria resulting from the constraints of an ecological niche, this looks quite different and research on domestic animals might even offer an experimental approach which would be of heuristic value. Homing pigeons could be an example of an evolutionary process that stresses the roles of adaptation and optimization in the sense of Maynard Smith [1982] and Gomulkiewicz [1998].

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Navigational Experience Affects Hippocampus Size in Homing Pigeons

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Key Words
Homing pigeon · Navigation · Hippocampus · Brain

Abstract

Homing (racing) pigeons (*Columba livia* f.d.) are well-known for their homing abilities, which are thought to be based on a genetic predisposition, multimodal learning and spatial cognition. On average, the hippocampus, a forebrain structure that processes spatial information, is larger in homing pigeons compared to other non-homing pigeon breeds or their wild ancestor, the rock dove. Here we show that this characteristic hippocampus volume is dependent on flying and navigational experience. Twenty homing pigeons originating from the same breeding stock were raised in the same loft under identical constraints. After fledging, 10 of them were allowed to fly around the loft, gain navigational experience and participate successfully in races. The other 10 stayed permanently in the loft and thus did not share the navigational skill experienced by the first group. After reaching sexual maturity, individuals of both groups were sacrificed and morphometric analyses were carried out to measure the volumes of total brain, telencephalon, hippocampus and 12 other brain structures. Individuals with experience in flying and navigation had an 11.2% larger hippocampus relative to the telencephalon compared to non-experienced individuals ($p = 0.028$). This effect is not seen in any of the other measured brain subdivisions. Given that plasticity in hippocampal volume has a genetic component, our results confirm that there is also an experience component, and that has certain implications for navigational ability. Evidently, experience is a precondition to full hippocampal development.

Introduction

Homing (racing) pigeons (*Columba livia* f.d.) are a breed of the domestic pigeon and well-known for their homing abilities, which allow them to return to their lofts from unknown release sites more than one hundred kilometers distant. Due to strong selection, the homing abilities of these pigeons are superior even to that of rock doves, the wild ancestor of homing pigeons [Alleva et al., 1975; Visalberghi et al., 1978], and are presumably based on a genetic predisposition, multimodal learning and spatial cognition [Lipp 1983; Wallraff 2001]. Although much is known about navigational skills and spatial cognition in birds, there are still open questions. Several orientation mechanisms – olfactory cues, visual landmarks, sun compass, earth's magnetic field – are known to be involved in homing behavior as well as parameters such as motivation and experience are also known to play roles

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[Papi et al., 1974; Visalberghi and Alleva 1975; Schmidt-König, 1990; Bingman, 1993]. But to date little is known about how and to what degree all these parameters interact and particularly how much they are influenced by individual life history.

On the neuronal level, the hippocampus plays a critical role in processing spatial information both in birds and in mammals [Rehkämper, 1981; Stephan et al., 1991; Bingman, 1993; Atoji et al., 2002; Jacobs, 2003; Nadel and Hardt, 2004] and Nadel and Willner [1989] indicated that early experience can alter the development and subsequent functioning of the hippocampus. It has been demonstrated that wild species with distinct navigational skills, as well as food-storing species, show relatively large hippocampi [Healy and Krebs, 1992; Sherry et al., 1992; Clayton and Krebs, 1994; Clayton, 1995], and that homing in homing pigeons depends on hippocampus function [Bingman et al., 2003]. On average the hippocampus in homing pigeons is larger than that in other non-homing pigeon breeds or their wild ancestor, the rock dove [Rehkämper et al., 1988, 2008]. The same relationship is also seen in the olfactory bulb, the neuronal basis for receiving and integrating olfactory cues [Rehkämper et al., 1988, 2008]. In addition, there are morphological and histological differences in hippocampal tissue in homing and non-homing pigeons [Shapiro and Wieraszko, 1996]. Thus, brain alterations in homing pigeons can be understood as an adaptation to homing. This view contrasts with those of Herre and Röhrs [1990], Kruska [1988] and Hemmer [1990] who describe domesticated animals as experiencing general sensory deprivation and thus always exhibiting brain (structure) size reductions when compared to their wild ancestral species.

It is the purpose of this paper to demonstrate that such a behavioral adaptation includes not only increases in the size of certain brain structures in homing pigeons in general but also individual increases during ontogenesis that are dependent upon experience. To date it has been shown that a relatively large hippocampal volume is associated with food-storing and food-retrieving experience [Clayton and Krebs, 1994; Clayton, 1996] and migratory experience [Healy et al., 1996]. Additionally, navigational skills as well as memory are needed for both food acquisition and migratory behavior. To date, the correlation between hippocampal size and navigational experience has not been studied in homing pigeons, which are representatives of a domesticated species. Thus, we report for the first time that in homing pigeons the characteristic hippocampus volume in relation to the telencephalon depends on navigational experience and associated flying behavior.

Material and Methods

Experimental Design

Twenty homing pigeons originating from the same breeding stock were raised in the same loft under identical conditions. At the time of fledging, the pigeons were randomly assigned to two experimental groups as follows: 10 (5 male, 5 female) of them were allowed to fly around the loft, gain navigational experience and participate successfully in races. This means that they participated in at least three (1 pigeon), but in as many as six (6 pigeons) or seven (3 pigeons) races with distances of 50–284 km. Thus, the whole flight performance of every pigeon varied between 479 and 1210 km.

The other 10 pigeons (5 male, 5 female) stayed permanently in the loft and thus did not share the navigational experiences of the first group. The size of the loft (108 × 140 × 200 cm) enabled these pigeons to fly, so that physical exercise was nearly equal between the two groups. Thus, this design of our study ensures that the two pigeon groups differed only with respect to free flying and homing/navigational experience.

Brain Preparation

After reaching sexual maturity, the brains of all 20 homing pigeons were investigated. After their body weights were determined, all individuals were sacrificed by an overdose of anesthesia and subsequently perfused with saline solution and a fixative (Bodian's solution) via the left ventricle. Brains were removed, weighed and embedded in paraffin. The brain weight was taken immediately (<60 min) after perfusion and the dissection weight was identical to the fresh brain weight [Stephan et al., 1981]. All brains were completely serially sectioned (20 μm) in a coronal plane. Every 5th section was mounted and stained for perikarya using a silver technique [Gallyas, 1971].

Morphometry

For morphometry the contours of the brain and brain subdivisions were drawn with a digital pen using a camera lucida. Then the resulting values were multiplied by the section thickness, the distance between the sections, and the conversion factor for shrinkage to obtain the fresh volume for each brain or brain subdivision [Stephan et al., 1981].

Six fundamental brain subdivisions (cerebellum, diencephalon, optic tectum, optic tract, tegmentum and telencephalon) were measured, followed by measurements of 8 telencephalic subdivisions: hyperpallium apicale, hyperpallium densocellulare, mesopallium, nidopallium (including entopallium and arcopallium), striatopallidal complex (including globus pallidus, lateral striatum, medial striatum and tuberculum olfactorium), hippocampus, septum and bulbus olfactorius. Figure 1 illustrates some of these areas. A definition of the borders of these areas is given by Rehkämper et al. [1991]. Based on these data the net brain volume was calculated as the sum of the single brain subdivisions. In contrast to brain volume, the net brain volume does not include the volume of leptomeninges, ventricles, choroid plexus and the remains of cranial brain nerves. All measurements were conducted blind, meaning that the investigator did not know which brain belonged to which individual pigeon or experimental group.

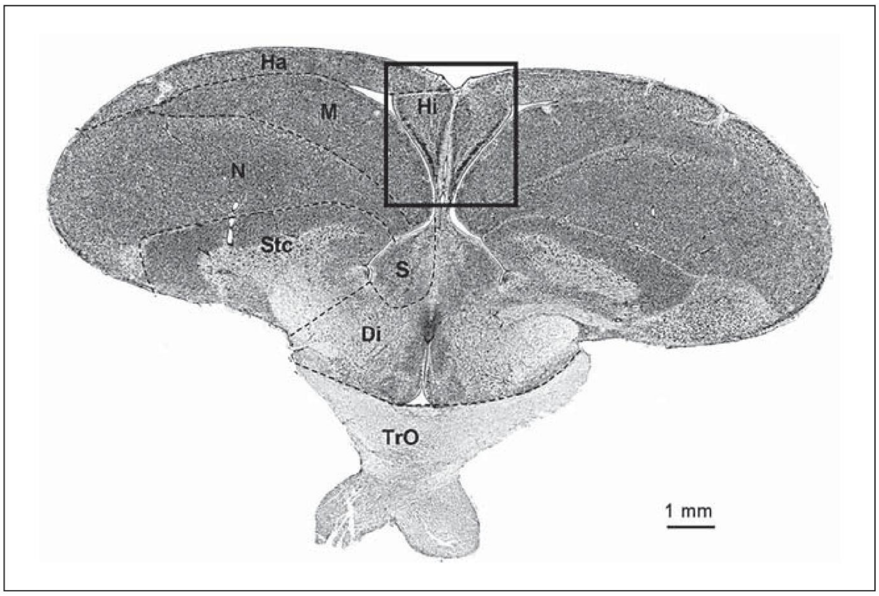

Fig. 1. Coronal section through the brain of a homing pigeon to illustrate selected subdivisions (Di = diencephalon; Hi = hippocampus; Ha = hyperpallium apicale; M = mesopallium; N = nidopallium; Stc = striatopallidal complex; S = septum; TrO = tractus opticus). Gallyas stain.

Volumetric Analyses

Volumetric data were analyzed by using a general linear model [Darlington, 1990]. The volumes of fundamental brain parts were compared in relation to net brain volume and the volumes of telencephalic subdivisions were related to the volume of the whole telencephalon. Thus, volume of brain subdivision was used as a dependent variable, treatment (experienced/non-experienced) as a categorical independent variable, and net brain volume or telencephalon volume as a (independent) covariate or confounding variable. The general linear model tests for effects of each of the independent variable, while keeping the other independent variables constant [Darlington and Smulders, 2001].

The original research reported herein was performed under the guidelines of the German law to prevent cruelty to animals.

Results

Average body weights, net brain volume and brain subdivision volumes in homing pigeons with and without navigational experience are given in table 1. The 10 pigeons with navigational experience had a mean body weight of 469.52 ± 39.60 g (mean ± SD), a mean net brain volume of 2,241.04 ± 139.84 mm^3, a telencephalon volume of 1,105.19 ± 87.60 mm^3 and a hippocampus volume of 43.43 ± 5.82 mm^3. The 10 pigeons without navigational experience had a mean body weight of 509.26 ± 42.62 g, a mean net brain volume of 2,282.39 ± 127.66 mm^3, a telencephalon volume of 1,126.64 ± 72.04 mm^3 and a hippocampus volume of 38.56 ± 4.47 mm^3.

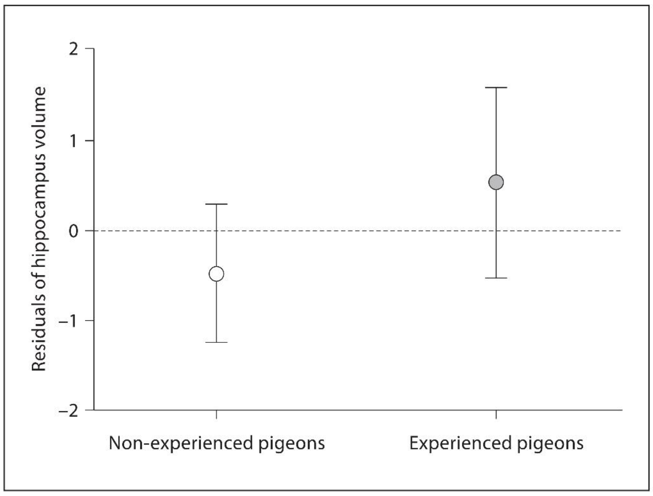

Fig. 2. Residuals (± SD) based on the general linear model with hippocampus volume in relation to telencephalon volume to illustrate the significant differences between experienced and non-experienced homing pigeons.

Individuals with experience of flying and navigation had an 11.2% larger hippocampus relative to the telencephalon compared to non-experienced individuals. The general linear model confirms a significant effect of navigational experience on relative hippocampus volume (F = 5.53, p = 0.028; fig. 2). This effect is not seen in any of the other measured brain subdivisions.

Table 1. Volumes of brain subdivisions (mm^3) and body weight (g)[1] with results from analysis (General Linear Model, GLM)

Subdivisions	Volumes		GLM results
	experienced pigeons (n = 10)	non-experienced pigeons (n = 10)	
Net brain volume	2,241.04±139.84	2,282.39±127.66	
Telencephalon	1,105.19±87.60	1,126.64±72.04	F = 0.05, p = 0.823
Diencephalon	148.85±4.42	153.16±7.31	F = 1.94, p = 0.182
Tractus opticus	64.34±6.52	64.09±9.08	F = 0.55, p = 0.471
Tectum	219.22±14.76	224.42±12.55	F = 0.23, p = 0.641
Tegmentum	338.38±18.37	336.95±22.14	F = 1.21, p = 0.286
Cerebellum	365.21±29.25	387.25±32.55	F = 2.22, p = 0.155
Hyperpallium apicale	141.32±11.40	147.77±12.92	F = 1.01, p = 0.330
Hyperpallium densocellulare	38.38±3.74	38.45±5.06	F = 0.03, p = 0.872
Mesopallium	195.53±23.84	199.83±19.86	F = 0.06, p = 0.806
Nidopallium	503.62±45.11	518.51±35.04	F = 0.98, p = 0.376
Striatopallidal complex	158.88±12.90	159.66±13.59	F = 0.15, p = 0.705
Hippocampus*	43.43±5.82	38.56±4.47	F = 5.73, p = 0.028
Septum	15.34±0.68	15.54±0.92	F = 0.06, p = 0.817
Bulbus olfactorius	8.64±0.87	8.37±0.89	F = 0.93, p = 0.350
Body weight, g	469.52±39.60	509.26±42.62	

[1] Values are means ± SD.
* p = 0.028.

Discussion

It is known that experience is an important factor determining the homing performance of homing pigeons. Free flying around the loft and training flights from distant locations were found to improve the homing success and frequently the initial orientation of test birds [Matthews, 1953; Lipp, 1983; Wallraff, 2001]. On their first flights, young birds become familiar with a variety of orientation cues and learn to make use of them (learning a 'navigational map') to help them return home faster and more reliably [Wiltschko, 1983].

The most important result of the present study is that the size of the relative hippocampus volume of homing pigeons depends on experience. It is indisputable that the hippocampus plays an important role in learning, spatial memory and spatial cognition not just in mammals [Stephan et al., 1991; Sherry et al., 1992; Rehkämper et al., 2001; Jacobs, 2003] but also in birds [Bingman, 1993; Atoji et al., 2002; Jacobs, 2003; Bingman et al., 2003, 2005]. Natural selection, sexual selection and artificial selection have resulted in an increase in the size of the hippocampus in a remarkably diverse group of animals that rely on spatial abilities to solve ecologically important problems, and there is a common relationship between relative hippocampus size and spatial ability [Sherry et al., 1992]. Standing out among mammals are elephant shrews with extraordinarily large hippocampi that are correlated with superior spatial cognition for remembering many sheltering places in large home ranges [Sauer, 1973; Rehkämper, 1981; Stephan et al., 1991; Rehkämper et al., 2001]. Strong selection by humans for homing ability led to a relatively larger hippocampus in homing pigeons, but what is new in our results is finding that an enlargement of the hippocampus can occur as a result of experience.

In our study we have not determined what is responsible for this increase in volume, but it would be interesting to see why the hippocampus might be larger. Existing cells could increase their cell body size or build up larger dendritic arbors, new neurons or glia could be added, or there could be increased vascularization. Interestingly, seasonal variation in hippocampus size has also been observed in birds [songbirds: Nottebohm, 1981; food-storing birds: Smulders et al., 1995].

Previous studies have shown that the hippocampus is plastic in response to specific kinds of sensory input, experience (learning) or hormonal influences [Cramer, 1988; Clayton and Krebs, 1994; Jacobs and Spencer, 1994]. In mammalian species an influence of experience on hippocampal volume has been demonstrated in rats [Cramer, 1988], but most studies with birds investigate food-storing birds and thus the effects of food-storing experience [Clayton and Krebs, 1994; Clayton, 1995, 1996]. An effect of migratory experience on hippocampal growth is seen in warblers [Healy et al., 1996]. In this study we have confirmed the plasticity of avian hippocampus in homing pigeons, and have shown for the first time that the hippocampus is also affected by navigational experience.

This finding is in line with the finding that pigeons raised while confined in an aviary have difficulties in perceiving spatial relationships among the landmarks in the home area, resulting in a less accurate spatial map and impaired navigation ability [Bingman and Mench, 1990; Gagliardo et al., 2007]. The hippocampus has been proposed to play a critical role in the neuronal regulation of a navigational system used by homing pigeons to locate their lofts once they are in the familiar area near home [Bingman and Mench, 1990; Gagliardo et al., 1999], and the exact formation of this navigational system depends on a bird's individual experience [Wiltschko, 1983]. Hippocampus-lesioned pigeons allowed to fly freely from the loft frequently get lost, probably because they are impaired at learning to navigate by familiar landmarks near the loft [Strasser et al., 1998]. Under laboratory conditions it can be seen that such pigeons are particularly unable to use geometric information in contrast to feature cues [Vargas et al., 2004]. But if young hippocampus-lesioned pigeons are allowed to fly freely during their first summer (during the time of navigational map learning) they can also learn a navigational map (or 'mosaic' map) indistinguishable from that of unlesioned pigeons, provided that they are allowed to receive atmospheric odors [Ioalè et al., 2000]. Thus it would be interesting to take a closer look at the volume of the olfactory bulb. Generally, the olfactory bulb of homing pigeons is enlarged in comparison to non-homing breeds or rock doves [Rehkämper et al., 1988, 2008]. But in our study both experimental pigeon groups received olfactory cues, i.e., atmospheric odors from around their loft, which resulted in our finding of no differences in olfactory bulb volume (see table 1). A detailed study between olfactory deprived pigeons and pigeons that are allowed to receive olfactory cues would be interesting for demonstrating the possible plasticity of the olfactory bulb.

It is a matter of fact that homing pigeons have extraordinary large hippocampi. Our data indicate that experience has an influence on that brain structure. Future analyses will address structural details and developmental mechanisms behind that increase. This is of general interest to most researchers in the comparative neuroanatomy field and homing pigeons as domesticated animals are a more than suitable model.

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Asymmetry of different brain structures in homing pigeons with and without navigational experience

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SUMMARY

Homing pigeons (*Columba livia* f.d.) are well-known for their homing abilities, and their brains seem to be functionally adapted to homing as exemplified, e.g. by their larger hippocampi and olfactory bulbs. Their hippocampus size is influenced by navigational experience, and, as in other birds, functional specialisation of the left and right hemispheres ('lateralisation') occurs in homing pigeons. To show in what way lateralisation is reflected in brain structure volume, and whether some lateralisation or asymmetry in homing pigeons is caused by experience, we compared brains of homing pigeons with and without navigational experience referring to this. Fourteen homing pigeons were raised under identical constraints. After fledging, seven of them were allowed to fly around the loft and participated successfully in races. The other seven stayed permanently in the loft and thus did not share the navigational experiences of the first group. After reaching sexual maturity, all individuals were killed and morphometric analyses were carried out to measure the volumes of five basic brain parts and eight telencephalic brain parts. Measurements of telencephalic brain parts and optic tectum were done separately for the left and right hemispheres. The comparison of left/right quotients of both groups reveal that pigeons with navigational experience show a smaller left mesopallium in comparison with the right mesopallium and pigeons without navigational experience a larger left mesopallium in comparison with the right one. Additionally, there are significant differences between left and right brain subdivisions within the two pigeon groups, namely a larger left hyperpallium apicale in both pigeon groups and a larger right nidopallium, left hippocampus and right optic tectum in pigeons with navigational experience. Pigeons without navigational experience did not show more significant differences between their left and right brain subdivisions. The results of our study confirm that the brain of homing pigeons is an example for mosaic evolution and indicates that lateralisation is correlated with individual life history (experience) and not exclusively based on heritable traits.

Key words: homing pigeon, lateralisation, asymmetry, brain, navigation, mosaic evolution.

INTRODUCTION

Functional specialisation of the left and right hemispheres of the brain ('lateralisation') was first found in humans (e.g. Broca, 1865; Geschwind and Galaburda, 1985) but has now been documented in a variety of species including birds (Nottebohm, 1970; Rogers, 1996; Vallortigara et al., 1996; Güntürkün, 1997).

Since the first evidence of functional lateralisation in birds, studies have documented right–left differences in avian visual processing (e.g. Rogers, 1996; Vallortigara et al., 1996; Güntürkün, 1997), auditory processing (e.g. Howard et al., 1980; Rogers and Anson, 1979), song production (Williams et al., 1992; Floody and Arnold, 1997; Poirier et al., 2009) and aspects of spatial learning and memory (e.g. Rashid and Andrews, 1989; Clayton and Krebs, 1994a; Ulrich et al., 1999; Gagliardo et al., 2001; Kahn and Bingman, 2004). A number of laboratory studies in birds have suggested that the right hemisphere may play a preferential role in global representation of space (by constructing a detailed organisational and topographical map) and learning and memory for global, distally located spatial information whereas the left hemisphere shows a preference for learning and remembering features of goal locations, encoding object-specific cues (by discriminating and categorising stimuli) and the representation of proximal cues (landmarks) used to locate a goal in space (Rashid and Andrew, 1989; Ulrich et al., 1999; Vallortigara et al., 1999; Clayton and Krebs, 1994a; Tommasi and Vallortigara, 2001; Prior et al., 2002). However, there are species-dependent differences (e.g. between chicks and pigeons), which have to be considered (Rogers and Deng, 1999; Tommasi and Vallortigara, 2001).

Such studies mostly describe functional cerebral lateralisation. Morphological asymmetries were described in different layers of the optic tectum (cell sizes) (Güntürkün, 1997) and in left and right hippocampi of homing pigeons (cell types, 'location cells' and 'path cells') (Hough and Bingman, 2004; Siegel et al., 2006).

Homing pigeons are well known for their homing abilities thought to be based on a genetic predisposition, multimodal learning, spatial cognition and motivation (Lipp, 1983; Wallraff, 2001; Cnotka et al., 2008; Mehlhorn and Rehkämper, 2009). Several orientation cues and mechanisms – olfactory cues, visual landmarks, sun compass, magnetic compass – are known to be involved in homing behaviour, and parameters such as motivation and experience are also known to be important for fast and successful homing (Papi et al., 1974; Visalberghi and Alleva, 1975; Schmidt-König, 1990; Bingman, 1993; Lipp, 1996; Walcott, 2005). The brain of homing pigeons is an example of mosaic evolution, which means that subsystems of the brain might follow different trends of (size) alteration independently from others (Mayr, 1963; Barton and Harvey, 2000; Rehkämper et al., 1988; Rehkämper et al., 2008). It seems to be functionally adapted to homing with several differences from other domestic pigeon breeds or their wild ancestors, the rock doves (*Columba livia*) (Haase et al., 1977; Rehkämper et al., 2008). These differences become manifest, for example, in larger hippocampi or olfactory bulbs, which are both involved in homing (Bingman et al., 2003; Bingman et al., 2005; Wallraff, 2005; Rehkämper et al., 2008). To date it has been shown that a relatively large hippocampal volume in food-storing birds is associated with food-storing experience (Clayton and Krebs, 1994b; Clayton, 1996), in migratory birds with migratory experience (Healy et al., 1996) and in homing pigeons with navigational experience (Cnotka et al., 2008).

To summarise, it is well known that three parameters characterise the brain of homing pigeons: (1) it is well adapted to homing, (2) it is (at least functionally) lateralised, and (3) it is plastic due to experience.

This leads to the question in what way lateralisation is reflected in homing pigeon brain structure volume and whether some lateralisation or asymmetry in homing pigeons is caused by experience. Thus, we compared brains of homing pigeons with and without navigational experience referring to this.

MATERIALS AND METHODS

Experimental design

Fourteen homing pigeons (*Columba livia*, Gmelin 1789) originating from the same breeding stock were raised in the same loft under identical constraints. The size of the loft (108 cm×140 cm×200 cm) gave all of the pigeons the possibility to fly. After fledging, seven of them (two males, five females) were allowed to leave the loft to fly around, gain navigational experience and participate successfully in pigeon races. This meant that they participated in at least three (one pigeon) but in as many as six (three pigeons) or seven (three pigeons) races with distances of 50–284 km. Thus, the whole flight performance of every pigeon varied between 479 km and 1210 km.

The other seven pigeons (two males, five females) stayed permanently in the loft and did not share the navigational experiences of the first group. However, the size of the loft enabled these pigeons to fly. Thus, the design of our study ensures that the two pigeon groups only differed with respect to free flying and homing experience.

Brain preparation

After reaching sexual maturity, all 14 individuals were killed with an overdose of anesthesia and subsequently perfused with saline solution and a fixative (Bodian's solution) (Romeis, 1989) *via* the left ventricle. All brains were removed and immediately weighed. After being embedded in paraffin, all brains were completely serially sectioned (20 μm) in a coronal plane. Every fifth section was mounted and stained for perikarya using a silver technique (Gallyas, 1971) that allows a clear and reproducible delineation of the different brain areas.

Measurements

For morphometry the contours of the brain and brain subdivisions were drawn with a digital pen using a camera lucida. To arrive at the fresh volume, the resulting values were multiplied by the section thickness and the distance between the sections. Because the brain shrinks considerably during histological processing, there are differences between the measured volume in serial sections and the fresh brain volume. The extent of shrinkage is different in each brain. To obtain comparable values, each (structural) volume was multiplied by the conversion factor for shrinkage (C), where C=volume fresh brain/sum of serial section volumes (Stephan et al., 1981).

Eight telencephalic brain subdivisions were considered: hyperpallium apicale, hyperpallium densocellulare, mesopallium, nidopallium (including entopallium and arcopallium), striatopallidal complex (including globus pallidus, lateral striatum, medial striatum and tuberculum olfactorium), hippocampus, septum and bulbus olfactorius. Fig. 1 illustrates some of these areas. All these measurements were done separately for the left and right hemispheres. Additionally six basic brain subdivisions (cerebellum, diencephalon, optic tectum, optic tract, tegmentum and whole telencephalon) were measured to calculate the net brain volume as the sum of all single brain subdivisions. In contrast to whole brain volume, the net brain volume does not include the volume of leptomeninges, ventricles, choroid plexus and remains of cranial nerves. Because of described morphological asymmetries in the optic tectum and its role in processing visual information (Güntürkün, 1997), measurements of optic tectum were done separately for the two hemispheres as well. All measurements were done blind, which meant that the investigator did not know which brain belonged to which individual pigeon.

Data analysis

Volumetric variables were assumed to be log-normally distributed and were described by geometric means ± standard deviation factors. This corresponds to the exponentiated means ± standard deviations of the log values. Relative differences between the left *versus* right telencephalic brain parts were calculated as quotients in each pigeon and were described by geometric means in both groups (experienced and non-experienced pigeons). Both groups were compared statistically by the t-test considering the logarithmised relative differences per pigeon.

As a secondary analysis paired t-tests were used to compare (log-) volumes on the left and right hand sides separated for both groups. 95% confidence intervals corresponding to the geometric means of the left and right telencephalic brain parts were presented graphically in both groups.

The level of significance was 5%. All tests were performed two-sided. For statistical calculations the software package SAS version 9.2 TS2M0 (SAS Institute, Cary, NC, USA) was used.

The original research reported herein was performed under the guidelines of the German law to prevent cruelty to animals.

RESULTS

Mean net brain volume and brain subdivision volumes (of the left and right hemispheres if available) in homing pigeons with and without navigational experience are given in Table 1. The seven pigeons with navigational experience had a (geometric) mean net brain volume of 2187.50±1.04 mm^3 and a telencephalon volume of 1070.24±1.05 mm^3. The seven pigeons without navigational experience had a mean net brain volume of 2244.06±1.04 mm^3 and a telencephalon volume of 1097.26±1.05 mm^3.

The comparison of the left/right quotients of both groups (Table 2) show one significant difference, i.e. pigeons with navigational experience show a smaller left mesopallium in comparison with the right mesopallium (0.953), pigeons without navigational experience show a larger left mesopallium in comparison with the right one (1.015). This difference is significant (Fig. 2A, t=2.241, P=0.045).

There are significant differences between left and right brain subdivisions in the two groups of experienced and unexperienced pigeons in the following brain structures: both, pigeons with and pigeons without navigational experience, show a larger left hyperpallium apicale in relation to the telencephalon (Fig. 2B, experienced pigeons: t=4.090, P=0.006; unexperienced pigeons:

Table 1. Volumes of (left/right) brain subdivisions (mm^3)

	Volumes			
	Experienced pigeons (*N*=7)		Unexperienced pigeons (*N*=7)	
Brain subdivisions	Left	Right	Left	Right
Telencephalon	534.10±1.05	536.14±1.06	551.01±1.05	546.25±1.06
Hyperpallium apicale	73.64±1.09	65.75±1.08	76.70±1.09	71.02±1.09
Hyperpallium densocellulare	19.07±1.12	19.88±1.11	18.78±1.19	18.94±1.15
Mesopallium	88.02±1.11	92.40±1.10	94.61±1.09	93.24±1.10
Nidopallium	240.03±1.04	245.20±1.04	250.93±1.06	254.00±1.06
Striatopallidal complex	77.24±1.08	77.60±1.10	76.59±1.06	76.12±1.06
Hippocampus	21.59±1.12	21.16±1.13	19.09±1.16	18.77±1.16
Septum	7.50±1.04	7.52±1.05	7.61±1.06	7.53±1.06
Bulbus olfactorius	4.08±1.08	4.23±1.11	4.05±1.12	4.03±1.14
Tectum opticum	108.45±1.07	110.44±1.08	109.14±1.04	111.04±1.04
Net brain volume	2187.18±1.04		2244.06±1.04	

Values are geometric means ± standard deviation factor.

t=4.933, *P*=0.003). Additionally, pigeons with navigational experience show a larger right nidopallium (*t*=2.663, *P*=0.037), a larger left hippocampus (Fig. 2C, *t*=2.500, *P*=0.047) and a larger right optic tectum (Fig. 2D, *t*=2.606, *P*=0.048). Pigeons without navigational experience did not show more significant differences.

DISCUSSION

The present study reveals that several structures in homing pigeons show a volumetrical lateralisation. Thereby, homing pigeons with navigational experience show a more lateralised brain than pigeons without navigational experience.

Before discussing the brain data in detail we would like to address the question whether these asymmetries reflect an enlargement of one side or a decrease of the other side. This is difficult to decide. We know that ontogenesis of the brain in mammals (and probably in birds too) is characterised by an initial overshooting generation of neuroblasts. Their survival depends on neurotrophic factors and on having established a ‘meaningful’ connection or not (Edelmann, 1993). In the latter case, the neuroblasts will degenerate and cause a volumetric decrease. A second aspect of neuronal ontogenesis is that the number of neurons in the adult brain might increase and/or develop new synaptical contacts, which could be mirrored by a volumetric enlargement. This has been shown particularly in birds (Nottebohm, 1970). Homing pigeons start flying at the age of 28 days. At this time they communicate with their parents and move around in the loft, which indicated a nicely developed brain. Thus, we think that at this time the remaining number of undifferentiated early neuroblasts is small. Based on these considerations, the asymmetries described here (and in previous papers) are thought to reflect an adaptive enlargement. However, in respect to function, it does not matter if the brain part under consideration is larger because of an increase of itself or a decrease of its counterpart.

The comparison of the left/right quotients of both groups revealed that pigeons with navigational experience show a smaller left mesopallium in comparison with the right one and pigeons without navigational experience a larger left mesopallium in comparison with the right one. This is (statistically) the most astonishing result because it incorporates the randomised groups. It means that the adaptive decrease of the mesopallium has taken place but it is in contrast to the hypothesis that the right hemisphere generally should mediate more emotional and instinctive reactions, while the left hemisphere deals with elaborated experience-based behaviours (MacNeilage et al., 2009; Valencia-Alfonso et al., 2009). Furthermore, particularly the mesopallium is associated with cognitive behaviour (Lefebvre et al., 2004) and thus an enlargement of the left mesopallium in pigeons without navigational experience is really unexpected given that navigation in birds is cognitive, particularly there is not necessarily any absolute volume difference

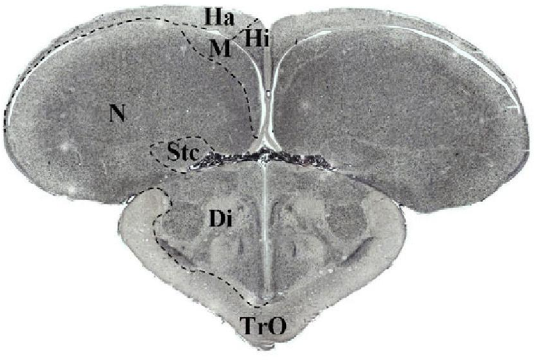

Fig. 1. Coronal section through the brain of a homing pigeon to illustrate selected subdivisions (Di=diencephalon, Ha=hyperpallium apicale, Hi=hippocampus, M=mesopallium, N=nidopallium, Stc=striatopallidal complex, TrO=tractus opticus).

Table 2. Quotients of left brain subdivision divided by right brain subdivision

	Quotients	
Brain subdivisions	Experienced pigeons (*N*=7)	Unexperienced pigeons (*N*=7)
Telencephalon	0.996±1.022	1.009±1.010
Hyperpallium apicale	1.120±1.076	1.080±1.042
Hyperpallium densocellulare	0.960±1.134	0.992±1.111
Mesopallium	**0.953±1.070**	**1.015±1.032**
Nidopallium	0.979±1.021	0.988±1.025
Striatopallidal complex	0.995±1.043	1.006±1.020
Hippocampus	1.037±1.040	1.017±1.055
Septum	0.997±1.063	1.011±1.036
Bulbus olfactorius	0.964±1.064	1.006±1.049
Tectum opticum	0.982±1.017	0.983±1.019

Values are geometric means ± standard deviation factor (bold: *t*=2.241, *P*=0.045).

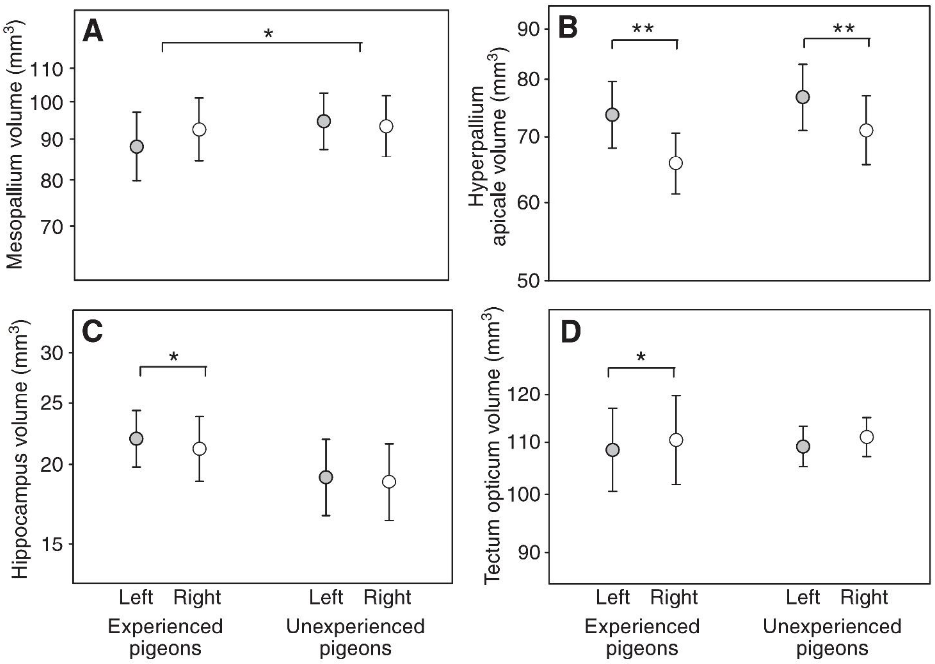

Fig. 2. Left and right brain structure volume of pigeons with and without navigational experience. Plots represent geometric means with 95% confidence interval. (A) Mesopallium, (B) hyperpallium apicale, (C) hippocampus, (D) optic tectum.

between the left mesopallium of the trained and untrained pigeons. However, more detailed analysis is needed for clarifying the role of the mesopallium in navigation.

A different explanation is proposed to understand the larger right nidopallium just in pigeons with navigational experience. Parts of the nidopallium are associative areas, involved in a lot of cognitive functions (Rehkämper and Zilles, 1991; Güntürkün, 2005) and presumed to be homologous to the mammalian isocortex (Lefebvre et al., 2004; Reiner et al., 2004).

Our nidopallium includes representation areas of sensory systems (Nieuwenhyus et al., 1998). As navigation is based on multimodal integration, we assume that the increase is due to an adaptive enlargement of such systems. This is supported by the fact that, e.g. the olfactory system is coined by an adaptive increase (Rehkämper et al., 2008). Up to date, a (functional) lateralisation or important role of the nidopallium in homing is unknown.

Two brain structures that are asymmetrical within the groups are as well multimodal but particularly involved with processing visual information: (1) the hyperpallium apicale, whereas the left one is larger in both pigeon groups in comparison with the right one, and (2) the optic tectum, whereas the right one is larger just in pigeons with navigational experience. Processing of visual stimuli by homing pigeons shows a strong lateralisation with superiority of the right eye and left hemisphere (Güntürkün, 1991; Ulrich et al., 1999; Prior et al., 2004). This hemispheric asymmetry might come about because the avian embryo lies in the egg with its left eye covered and its right eye exposed to light (Rogers, 1990). Such an asymmetry depends on light exposure and is minimised or changed by the absence of light during development (Rogers, 1982; Rogers, 1990; Andrew et al., 2009). In pigeons, the optic nerves almost completely decussate at the level of the chiasm, so the visual input to the right eye is processed more or less entirely by the left hemisphere (Nieuwenhuys et al., 1998). Similar to what occurs in mammals, processing visual information in pigeons occurs *via* two different main pathways: the thalamofugal and tectofugal pathway (Karten, 1979). But in contrast to mammals, the major part of visual information in birds uses the tectofugal way, which comprises the optic tectum, the n. rotundus and the entopallium as its telencephalic target. The thalamofugal pathway projects *via* the dorsal thalamus into the Wulst, which consists of the hyperpallia apicale, densocellulare and intercalatum. In birds it is concerned, inter alia, with processing visual stimuli for orientation (Güntürkün, 1991; Shimizu and Bowers, 1999). The hyperpallium apicale as a whole is not generally larger in pigeons with navigational experience although it is involved in processing information for successful homing (Cnotka et al., 2008). It is not even generally larger in homing pigeons in comparison with other non-homing pigeons (Rehkämper et al., 2008). Our finding of a larger hyperpallium apicale on the left hemisphere in both pigeon groups indicates that the hyperpallium apicale is lateralised in homing pigeons in general and it demonstrates for the first time a (volumetrical) lateralisation in the thalamofugal system in pigeons. Thus, it could be another adaptation on homing but without being larger or being sensitive to experience.

Several authors describe morphological and functional asymmetries in the tectofugal visual system of pigeons (Güntürkün, 1997; Skiba et al., 2002; Nardi and Bingmann, 2007) but not for the thalamofugal visual system; however, the larger right optic tectum in pigeons with navigational experience is difficult to explain. Functional asymmetries in the tectofugal visual system of pigeons are described rather with superiority of the left hemisphere (Güntürkün, 1997; Skiba et al., 2002; Nardi and Bingman, 2007). However, Rogers (Rogers, 2009) argues that lateralisation patterns might depend on hemispheric asymmetries in sensory processing, which is in line with observations by Valencia-Alfonso et al. who featured the pigeon as a model system of the hemispheric lateralisation of visual abilities (Valencia-Alfonso et al., 2009). They described functional asymmetries in the whole visual system of the pigeon and speculated that these asymmetries depend on the interplay of descending and ascending visual information streams (between telencephalic and subtelencephalic structures).

As far as we know, to date, the only structure sensitive to navigational experience is the hippocampus (Cnotka et al., 2008), which shows inter alia functional lateralisation (Gagliardo et al., 2001; Gagliardo et al., 2002; Gagliardo et al., 2005). The left hippocampus might play a more important role in the representation of a goal location in terms of environmental shape/geometry (Gagliardo et al., 2001; Gagliardo et al., 2002; Gagliardo et al., 2005), and Nardi and Bingman (Nardi and Bingman, 2007) proposed a relationship to the asymmetrical organisation of the tectofugal system whereas the left forebrain hemisphere, and therewith the left hippocampus, gets a higher degree of whole-field visual representation. Interestingly, this is in contrast to what has been described in chicks, which show a lateralisation in the thalamofugal system and a dominance of the right hemisphere for encoding geometric information (Rogers and Deng, 1999; Tommasi and Vallortigara, 2001; Tommasi and Vallortigara, 2004; Koshiba et al., 2003; Della Chiesa et al., 2006). The right hippocampus in homing pigeons appears to play an important role in local navigation near the loft, which is probably based on familiar landmarks (Gagliardo et al., 2001; Gagliardo et al., 2002; Gagliardo et al., 2005).

A morphological lateralisation of the hippocampus has been described by Hough and Bingman (Hough and Bingman, 2004; Hough and Bingman, 2008) and Siegel et al. (Siegel et al., 2006) (see Introduction), and in our study, the hippocampus shows a volumetrical lateralisation on the left hemisphere in pigeons with navigational experience. Recently, we showed that the hippocampus in homing pigeons with navigational experience is enlarged (Cnotka et al., 2008), and now we have replicated the training effect on hippocampal volume by showing that there is also a lateralisation, which is caused by experience.

It is known that there are several, mostly environmental, factors such as light exposure, body posture, social rearing or testosterone exposure that could influence the degree of lateralisation during ontogenesis (Andrew et al., 2009; Pfannkuche et al., 2009; Schaafsma et al., 2009). Navigational experience seems to be a further influencing factor that could even induce a lateralisation seen as volumetrical asymmetry.

It is speculated that lateralisation is ancient, closely associated with the bilateral symmetrical design of the brain (Vallortigara et al., 1999; MacNeilage et al., 2009). Among other advantages, the specialisation of the two sides of the brain has been supposed to increase neural efficiency by avoiding unnecessary duplication of neural circuitry and reducing interference between control systems (Rogers, 2000; Vallortigara and Rogers, 2005; Ghirlanda and Vallortigara, 2009; Tommasi, 2009). It has been shown that species that show gregarious behaviour are lateralised. Apparently, sociality and gregarious behaviour could have provided the constraints for a directional selection in favour of the asymmetries (Vallortigara et al., 1999; Rice, 2004). Solitary species are more likely to show lateralisation just in a few individuals of a population but not in general (Vallortigara et al., 1999; Halpern et al., 2005). The reasons for this are unclear but homing pigeons are gregarious.

The 'mosaic theory' suggests that the expansion of specific brain regions can occur independently of other regions (Barton and Harvey, 2000). Several examples of this are provided by Rehkämper et al. (Rehkämper et al., 2001), and include greater expansion of olfactory, spatial and somatosensory regions than of other brain regions. The results of the present study confirm that the brain of homing pigeons is an example for mosaic evolution under domestication (Rehkämper et al., 2008). If the brain composition of homing pigeons is represented by the 'developmental constraints theory' (Finlay and Darlington, 1995), we had to expect that changes in the size of one brain structure would be correlated with changes in all other brain structures. Recently, mosaic evolution has been demonstrated for the brain of wild mammals (Barton and Harvey, 2000), bats and whales (Clark et al., 2001) and wild avian species (Iwaniuk et al., 2004; Iwaniuk and Hurd, 2005; Charvet and Striedter, 2009), and it seems to be that mosaic evolution characterises the diversification of avian and mammalian brain composition without excluding domesticated species. Apparently, it is not just the subsystems of the brain that might follow different trends of alteration independently from others but even the left or right parts of a subsystem. Our study indicates that experience could influence the degree of mosaic evolution. Apparently, under the conditions of free flying and covering longer distances, the neural efficiency of several brain structures could be increased by lateralisation, and the data given in the literature and our own findings indicate that lateralisation is correlated with individual life history (experience) of a pigeon. The role of a genetic determination remains unclear. The role of experience must be investigated further if its evolution is of interest because modern evolutionary theory is primarily based on heritable traits rather than on acquired characters (Vincent and Brown, 2005).

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RESEARCH ARTICLE

The orientation of homing pigeons (*Columba livia* f.d.) with and without navigational experience in a two-dimensional environment

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Abstract

Homing pigeons are known for their excellent homing ability, and their brains seem to be functionally adapted to homing. It is known that pigeons with navigational experience show a larger hippocampus and also a more lateralised brain than pigeons without navigational experience. So we hypothesized that experience may have an influence also on orientation ability. We examined two groups of pigeons (11 with navigational experience and 17 without) in a standard operant chamber with a touch screen monitor showing a 2-D schematic of a rectangular environment (as "geometric" information) and one uniquely shaped and colored feature in each corner (as "landmark" information). Pigeons were trained first for pecking on one of these features and then we examined their ability to encode geometric and landmark information in four tests by modifying the rectangular environment. All tests were done under binocular and monocular viewing to test hemispheric dominance. The number of pecks was counted for analysis. Results show that generally both groups orientate on the basis of landmarks and the geometry of environment, but landmark information was preferred. Pigeons with navigational experience did not perform better on the tests but showed a better conjunction of the different kinds of information. Significant differences between monocular and binocular viewing were detected particularly in pigeons without navigational experience on two tests with reduced information. Our data suggest that the conjunction of geometric and landmark information might be integrated after processing separately in each hemisphere and that this process is influenced by experience.

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Introduction

A large amount of research has been conducted to understand which mechanisms and environmental properties enable animals to navigate accurately [1,2]. Many studies have shown that animals can encode and use multiple sources of information to locate a goal. For navigation within a familiar environment e.g., visual landmarks are an important source of information and are used by many species, including birds, [3–6]. Additionally, several studies have revealed that the geometry as defined by continuous surfaces can also deliver an important cue for an animal to obtain a sense of bearing for orientation [3,7,8,9,10]. However, the extent to which landmark and geometric information are relied upon and how much of the available information is actually used seems to differ across species and with experience [7,11,12].

Homing pigeons are an excellent model for investigating spatial cognition and/or orientation mechanisms. They use several orientation mechanisms (e.g. sun compass, magnetic compass, olfactory cues), but there is a general agreement that pigeons rely at least on visual cues or landmarks for flights within their familiar home ranges (<5 km) or for finding their home loft from familiar nearby releasing sites [2,13–17]. Kelly et al. [4] have already shown that Silver King pigeons are able to encode landmark and geometric information in an experimental environment (rectangular enclosure with three-dimensional objects or two-dimensional panels in each corner). However, the extent to which the pigeons later relied on geometric and landmark information is influenced by the bird's initial experience in the experimental situation, e.g. whether they were trained with or without landmark information before being tested with landmark and/or geometric information. Most of these studies have used a navigable open-field task, a kind of "spatial arena" in the form of a rectangular enclosed container. That pigeons are able to re-orientate, at least under certain condition, according to configural geometry in a rectangular array of landmarks was also shown by Pecchia et al. [18]. The role of landmarks and geometry in pigeon spatial cognition has also been investigated by using two-dimensional touch-screens [19]. It is quite apparent that encoding information within a three-dimensional (3-D) rectangular room could differ from encoding information within a two-dimensional (2-D) touch-screen task, because food is not found at the goal but instead dropped in a feeder in a different location and the search space is vertical and viewed at close range. Thus, the touch-screen task presents stimuli mainly to the short-distance binocular frontal field of the pigeon whereas in a 3-D rectangular room (or in natural situations) also the long-range monocular fields are called into play [20,21]. Kelly & Spetch [19] also used a touch-screen task conducted within a standard operant chamber. They trained pigeons to search for a hidden target area in images showing a schematic rectangular environment (served as geometric information). Various graphic stimuli in the corners of the rectangle served as landmarks. They revealed that pigeons are able to use the rectangular properties to locate the goal and that they could also use a single featural cue at an incorrect corner to distinguish between the correct corner and the geometrically equivalent corner.

Previous studies have mostly used Silver King pigeons, which were originally bred for meat production and have a huge habitus and limited flying and orientation capabilities. Thus, these animals are not really appropriate to investigate orientation. In the present study we used for the first time homing pigeons originated from high performance racing breeds and thus, with strong navigational skills. Corresponding to their excellent homing abilities, the brains of homing pigeons are well adapted to homing with e.g. larger hippocampi and olfactory bulbs in comparison to other pigeon breeds or even rock doves, the wild ancestor of homing pigeons [22,23]. In a previous study, we revealed that hippocampal volume depends on navigational experience and associated flying. Pigeons with a lot of navigational experience have a larger hippocampus volume than non-experienced or less experienced pigeons [24]. This was consistent with earlier findings that homing has its structural base in the hippocampus [2,25]. Hippocampus lesion experiments in homing pigeons showed that the hippocampus appears to be essential for the learning of map-like, spatial representations of environmental stimuli used for navigation and complements the navigational map of the homing pigeon. Under laboratory conditions, it can be seen that hippocampus-lesioned pigeons are particularly unable to use geometric information in contrast to feature cues [26].

Furthermore, we previously showed that experience not just has an influence on hippocampus volume, but also on brain lateralization which is reflected in homing pigeons' brain structure volume [27]. Pigeons with navigational experience show a more lateralized brain than pigeons without navigational experience. The brain structures affected are the hippocampus, the apical hyperpallium, the nidopallium, and the mesopallium. These structures are all involved in processing spatial or visual information [28,29,30]. Functional cerebral lateralization has been well documented in many species including birds [31,32]. Studies have documented right-left differences also in avian visual processing [33,34,35] and aspects of spatial learning and memory [36–41].

In the present study, we investigated how navigationally experienced and non-experienced pigeons encode featural (landmark) and geometric information when presented with a 2-D schematic of a rectangular environment, based on Kelly & Spetch [19]. This study is of interest because it complements previous investigations in pigeons that have examined the use of discrete landmarks for spatial search within 2-D touch-screen environments. But here, we used homing pigeons whose navigational abilities topped all other pigeon breeds respectively such as fancy or non-homing breeds like Silver King pigeons. The homing pigeons of the present study were bred for highly competitive pigeon races with distances up to 800 km and therefore should have strong navigational skills. Using such pigeons is an outstanding feature of this study.

Besides, the pigeons carried out all experiments first with both eyes and then again with monocular occlusion. Diekamp et al. [42] have demonstrated a substantial effect of monocular occlusion on homing performance, which corresponds to anatomical lateralization. In pigeons, visual information crosses completely to the contralateral optic tectum and the contralateral telencephalic hemisphere, and there are no large interhemispheric commissures as seen in mammals [30]. Thus, visual input to the right eye is processed mainly in the left brain hemisphere, and visual signals from the left eye are processed in the right brain hemisphere. Surely, there are as well connections between e.g. the optic tectum and the nucleus rotundus of both hemispheres and this might affect the lateralization of information taken in by the different eyes including behavioural consequences [43,44], but nonetheless, the design of this study should provide insights into the functional lateralization of the brain as well as which hemisphere encodes geometric or featural information.

We anticipated that non-experienced pigeons would show a poorer or at least different performance in comparison to experienced pigeons. Furthermore, we expected that the results would differ depending on binocular or monocular viewing.

Materials and methods

Subjects

Twenty-eight homing pigeons (*Columba livia* f.d.) originating from the same breeding stock of our own pigeon breed were raised in the same loft under identical conditions. After fledging, they were randomly assigned to two experimental groups: 17 of them (9 males, 8 females) were allowed to leave the loft to fly around, gained navigational experience, and participated successfully in pigeon races. This meant that they participated in at least 6 (four pigeons) to 10 (seven pigeons) races with distances of 50–284 km. The other six pigeons participated in 7 (three pigeons) or 8 (three pigeons) races. Thus, the whole flight performance of every pigeon varied between 959 km and 1119 km.

The other 11 pigeons (5 males, 6 females) stayed permanently in the loft and did not acquire the navigational experience of the first group. Yet the size of the loft (250 cm X 190 cm X 190 cm) did still allow these pigeons to fly. Thus, the design of our study ensured that the two pigeon groups differed only with respect to free flying and homing experience. All pigeons were at least six months old before the tests began and experimentally naïve with spatial search tasks. The daily requirement of food was estimated and after the start of the experiment, was provided only in the operant chamber. Grit and water were provided ad libitum.

Apparatus

The experimental apparatus was a custom-built operant chamber of 34 cm x 33 cm x 26 cm (Biobserve; Bonn, Germany). A color touch-screen monitor (screen size: 25.654 cm, Faytech; Göttingen, Germany) was placed inside the box against the front side. The touch-screen monitor was programmed to detect individual responses (pecks). Food rewards were presented using a standard pigeon feeder, located on the front side of the chamber under the monitor. A small lamp illuminated the feeder when a reward was available. The chamber was connected to a personal computer located next to it. This computer controlled all of the experimental contingencies and recorded the responses. The interior of the chamber was visually monitored on an external screen (LCD TV; Lenco; Nettetal, Germany) fed by a camera (CMOS Color Camera; Conrad Electronics; Hirschau, Germany), which was attached above a transparent window in the roof of the chamber.

Experimental design

Preliminary procedure. All the pigeons received several sessions of training (one session a day per bird) to establish reliable pecking at the monitor. Initially, the pigeons were habituated to the chamber and learned to get food in the chamber by using the pigeon feeder (*shaping*). No stimulus was presented and food was available during the session time which lasted 10 minutes in *shaping*. During the following *autoshaping*, a white square of 30 mm (first step) or 10 mm (second step) was intermittently presented in the middle of the screen against a black background, for 40 trials per session, with a 30 second intertrial intervals. The white square remained on the screen until the pigeon pecked at the square or 10 seconds had elapsed, and then food was presented. If the pigeon pecked the black background during the intertrial interval, the 30 second sequence was interrupted, and the square was presented immediately. After reliable pecking was established (20 or more pecked trials out of the total of 40), the pigeon got food only by pecking the square. Now, the pigeon had to peck the square for a trial to be completed. Again after 20 or more pecked trials, the size of the square was reduced from 30 mm to 10 mm. After the pigeon had completed here at least 20 trials within one session, *autoshaping* was finished and *pretraining* began. If the pigeon did not peck the square for 30 days/30 sessions, it was excluded from experiment. Images for *pretraining* presented a black background with a grey rectangle. Four uniquely colored and shaped landmarks/features (blue square, green circle, yellow star, red triangle) were presented adjacent to the four corners of the rectangle, and each pigeon was randomly assigned one of the four possible corners (associated with one landmark/feature). These four landmarks/features remained visible for all 40 trials per session during *pretraining*. In *pretraining*, the assigned corner of the rectangle contained a white response square (1 cm x 1cm, Fig 1A). Pecks to the white response square were immediately reinforced. *Pretraining* continued until a pigeon pecked the square at least 32 trials (out of the total of 40) on two consecutive sessions. The stimulus rotated clockwise during each experimental session (Fig 1A), and the pigeons were permitted to use both eyes.

In the following *training*, all corners of the rectangle contained a white response square (Fig 1B), but only pecking the correct (assigned) response square was rewarded and completed a trial successfully. *Training* continued until a pigeon completed successfully at least 32 trials (out of the total of 40) on two consecutive sessions. The stimulus rotated clockwise during each experimental session (Fig 1B), and the pigeons were permitted to use both eyes.

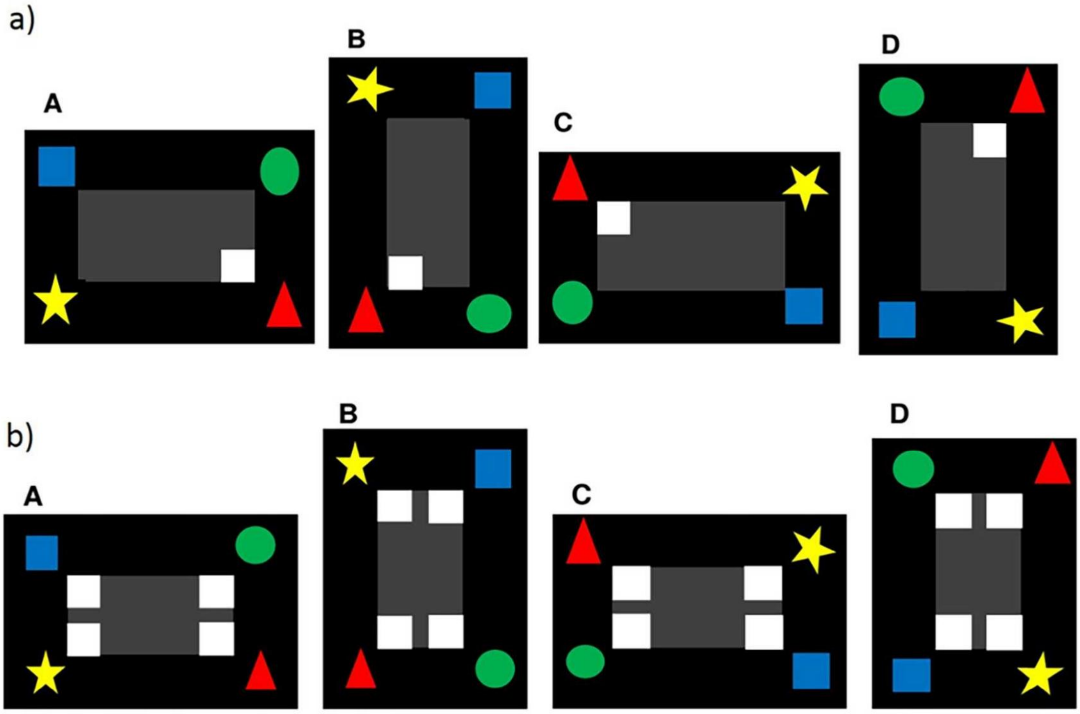

Fig 1. Examples of the stimuli used in *pretraining* (a) and *training* (b). In this example, the red triangle was reinforced. The stimulus rotated clockwise during the experimental session (A: 0˚; B: 90˚; C: 180˚; D: 270˚), and the pigeons used both eyes.

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Thus, after *training*, all pigeons were conditioned to get food by pecking on one response square which was associated with geometric information from the rectangle (e.g. long side left, short side right of the correct corner/feature) as well as a unique feature or "landmark".

Tests. After *training* all pigeons had to complete four *tests* (one test per day and bird) with again 40 trials total per test. Every *test* consisted of four test cycles, each with six *training* trials followed by four *test* trials. In the *test* trials (as well as in the *training* trials), the pigeons were also rewarded for pecking their assigned corner with respect to their assigned feature/landmark.

To examine whether featural and geometric representations would withstand spatial translations, we carried out as well a *Novel Perspective Test* where the same images were presented as in the training, but now in the lower left or right part of the touch-screen monitor.

Each of the four *tests* was carried out twice, and there were three testing conditions: binocular viewing, left eye occluded, right eye occluded. Thus, each test was done six times in total. For the monocular viewing, all pigeons were fitted with a ring of Velcro strip, attached around both eyes with "Precision Lash Adhesive" (Fing'rs; Stuttgart, Germany). Just before each experimental session, an eyepatch of Velcro strip was attached on this ring and covered the eye completely. This eyepatch was removed immediately after each session. For half of the pigeons, the order of the sessions per test was as follows: binocular viewing, left eye occluded, right eye occluded, binocular viewing, right eye occluded, left eye occluded. For the other half of the pigeons, the order of the sessions per test was: binocular viewing, right eye occluded, left eye occluded, binocular viewing, left eye occluded, right eye occluded. To complete a test session, a pigeon was required to peck during at least 12 test trials, independently from the choice.

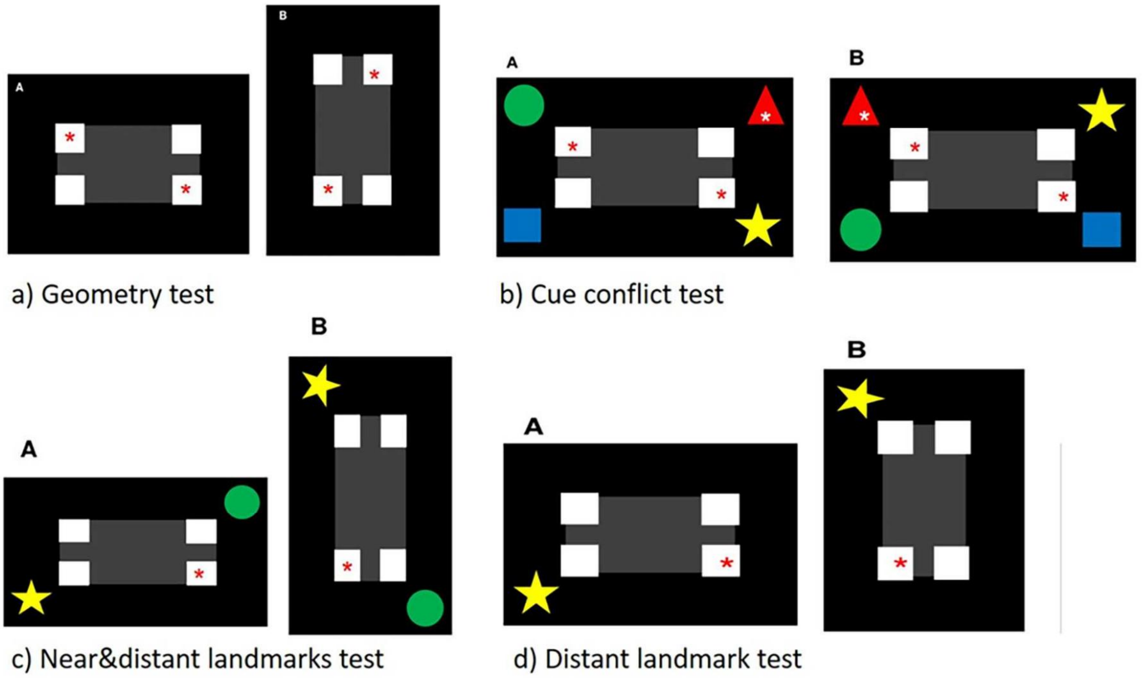

Fig 2. Examples of the stimuli used in the tests. For better demonstration, red (and white) asterisks show the rewarded corner(s)/features (here the red triangle) but were not visible for the pigeon during the test. The stimulus rotated clockwise; two different arrangements are shown (A: 0˚; B: 90˚).

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The four tests were as follows.

1. Geometry test (Fig 2A)
   Here, all features/landmarks were removed, so only geometric information was available. Because of this, there were now two correct choices possible, because two corners had the assigned/correct geometric information. Thus, the probability of choosing the correct corner by chance was 50%.

2. Cue Conflict test (Fig 2B)
   In the *cue conflict test*, the features/landmarks rotated counter clockwise around the rectangle. So, there are positions where there was a discrepancy between featural and geometrical information. Here, the correct feature/landmark was not in the corner with the correct geometric information. The pigeons had to decide which kind of information was more important for them for selecting a corner. We laid our focus on the featural information and rewarded the corner with the correct (assigned) feature/landmark. Thus, probability of choosing the correct (landmark) corner by chance was 25%.

3. Near & distant landmarks test (Fig 2C)
   In the *near & distant landmarks test*, the correct feature/landmark and the feature/landmark of the diagonal corner were removed. Thus, both features with the correct geometric information were removed. The other two features/landmarks–the one at the end of the short side of the rectangle (*near* to the correct corner) and the one at the end of the long side of the rectangle (*distant* to the correct corner)–were still shown. The probability of choosing the correct corner by chance was 25%.

4. Distant landmark only test (Fig 2D)
   In the *distant landmark only test*, three features/landmarks were removed: the correct one, the feature/landmark of the diagonal corner and the feature/landmark near to the correct corner (at the end of the short side of the rectangle). The probability of choosing the correct corner by chance was 25%.

Both *landmark tests* were to check whether the pigeons also use features for their choice, which were not rewarded or whether they also learned information about the relative positions of the other landmarks and the goal.

Data analysis

For analysis, the number of correct pecks was counted and compared in relation to the total number of pecks. We calculated the percentage of choices ("% choice") made to a particular corner averaged over all pigeons in the particular study group. To rule out the possibility that the pigeons chose the corner/landmark by chance, an ANOVA followed by Fisher's least significance test (LSD) was first used to compare the test data of both groups to the "by chance" probability of 50% (*geometry test*) or 25% (all other tests). After this, the data were compared statistically by t-test, or ANOVA (on ranks) for comparisons between the groups. Comparisons within the groups were done with parametric and non-parametric tests for dependent data, namely paired t-test, and (Friedman) Repeated Measures Analysis of Variance (on ranks) (FRM ANOVA, RM ANOVA). The level of significance was actual 5%, but for test analyses, we adjusted the alpha level to account for multiple comparisons using the Bonferroni correction; the alpha level was thus set to 0.004 (comparisons between the groups) or to 0.003 (comparisons within the groups). The software package SigmaPlot/SigmaStat version 12.0 was used for all statistical calculations.

All applicable international, national, and/or institutional guidelines for the care and use of animals were followed. The study was approved by the Committee on the Ethics of Animal Experiments of the state of North Rhine-Westphalia (Ref. 84–02.04.2013.A226).

Results

Preliminary procedure

Non-experienced pigeons needed significantly more time than experienced pigeons to habituate to the chamber and the experimental situation (mean±s.d.): 7.6±1.11 vs. 2.9±0.69 days to feed in the chamber (*shaping*), t-test: t = 3.868, $p<0.001$. Of the birds that completed autoshaping, there were no significant differences between the groups in the number of days they needed before starting to peck the touch-screen. But 4 of the 11 (36.37%) non-experienced and 7 of the 17 (41.18%) experienced pigeons had to be excluded from experiment because of nonfulfillment of the criteria for successful *autoshaping*: they did not learn to peck the touch-screen. In addition, non-experienced pigeons needed significantly more time (7.6±2.76 days) for completing the *training* (Fig 3), both, in comparison to their *pretraining* (4.0±2.00 days, paired t-test: t = -2.855, p = 0.029) and in comparison to training time of experienced pigeons (3.25±2.375 days, t-test: t = 3.261, p = 0.006).

We did not find significant differences between the groups and/or the different viewing conditions in the *Novel Perspective Tests.* Because of this, and comparable numbers of correct choices as in the regular training, we assumed that both, featural and geometric representations withstood spatial translations and continued with the *tests*.

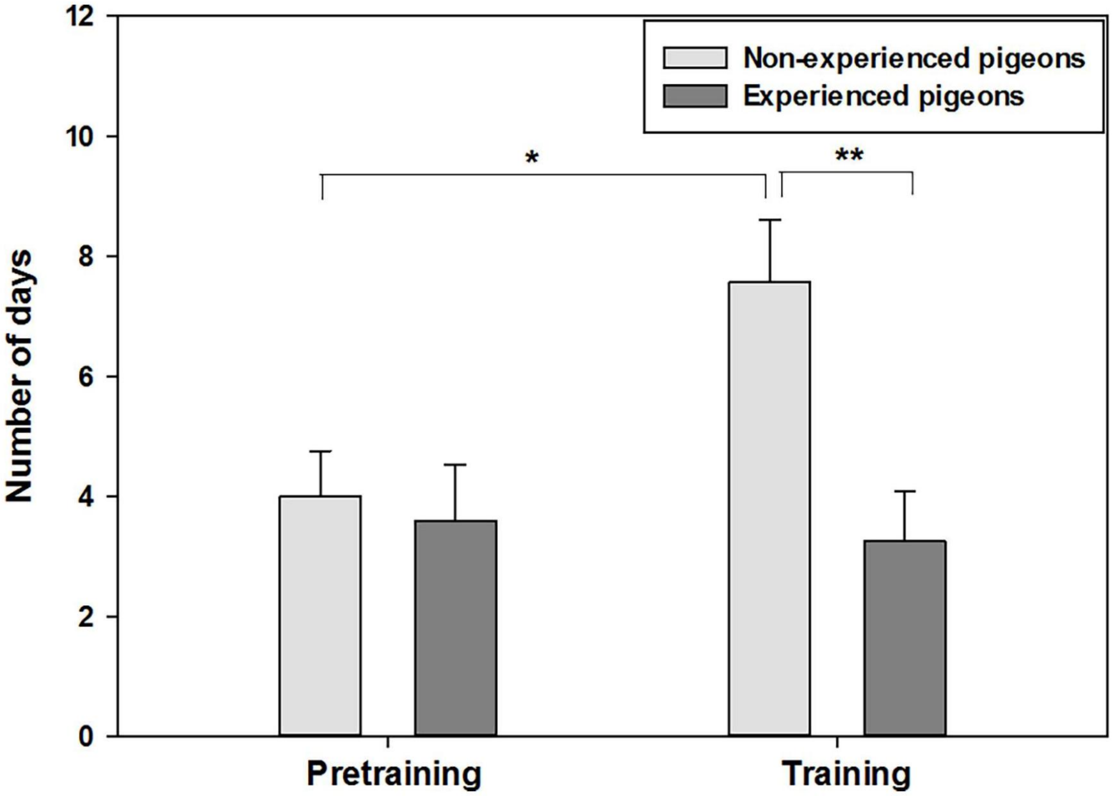

Fig 3. Required days for *pretraining* and *training* of non-experienced (n = 7) and experienced pigeons (n = 10). Error bars represent the standard errors of the mean (* = 0.029, ** = 0.006).

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Tests

(1) Geometry test. Experienced pigeons did not show significantly more correct choices than non-experienced pigeons (Fig 4, Table 1), (t-test, viewing with both eyes: t = -2.608, p = 0.020; viewing with the left eye: t = -2.373, p = 0.031; viewing with the right eye: t = -2.755, p = 0.015). The number of correct choices in the *geometry test* was always significantly above 50% (the probability of choosing the correct corner by chance), regardless of whether the pigeons used both eyes or just one eye (ANOVA/Fisher-test (LSD), S1 Table).

(2) Cue conflict test. There were no significant differences between the two groups of pigeons in the *cue conflict test* (Fig 4, t-test, viewing with both eyes: t = 1.260, p = 0.227; viewing with the left eye: t = 0.574, p = 0.287; viewing with the right eye: t = 0.535, p = 0.601).

The *cue conflict test*, where the features rotated clockwise around the rectangle, showed that both pigeon groups preferred choosing the corner on the basis of landmark information and not on geometrical information (Fig 5). They pecked the corner with the correct feature significantly more often in comparison to the other corners, even though the geometric information at that corner was incorrect (FRM ANOVA on ranks, S2 Table).

The number of choices of the correct feature/landmark in the *cue conflict test* was always significantly above 25% (the probability of choosing the corner by chance), regardless of whether the pigeons used both eyes or just one eye (ANOVA/Fisher-test (LSD), S3 Table).

(3) Near & distant landmarks test, (4) distant landmark only test. In the *near & distant landmarks test*, both features with the correct geometric information (the correct feature and the feature of the diagonal corner) were removed. In the *distant landmark only test*, the feature

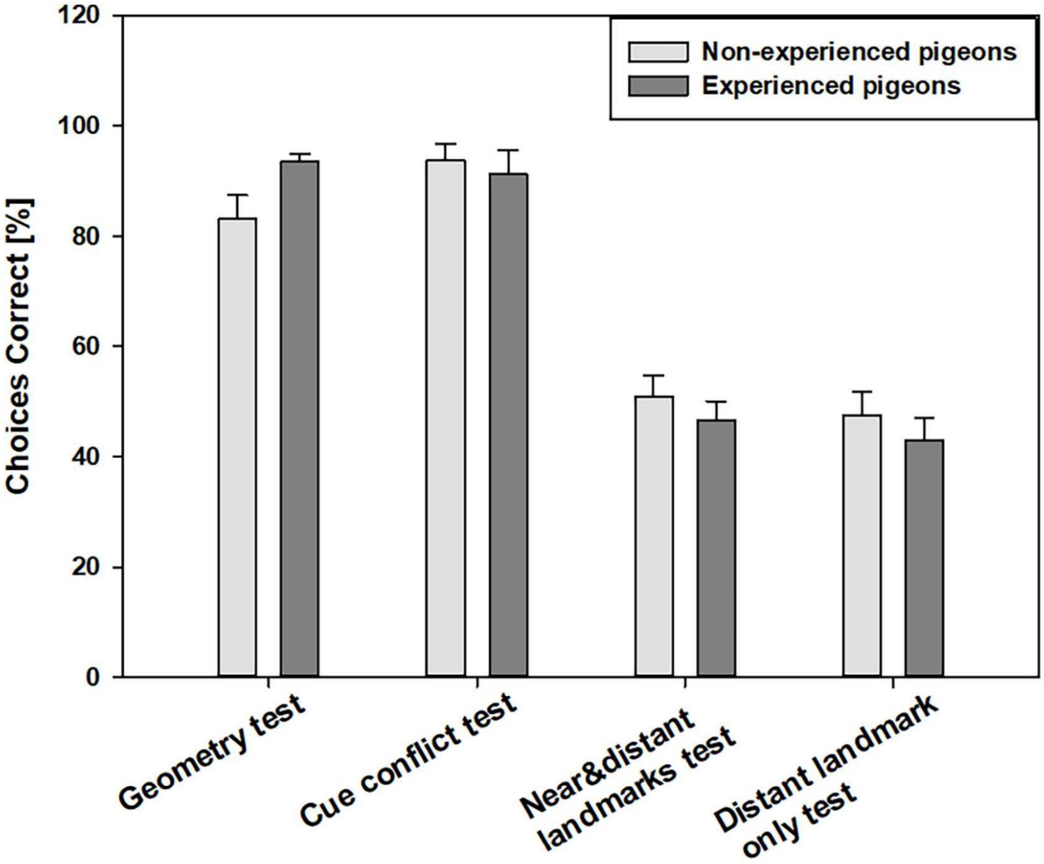

Fig 4. Percentages of choices made to the correct corner (*cue conflict test*: choice of the correct feature/ landmark) averaged over all non-experienced (n = 7) and experienced pigeons (n = 10) in the various tests with viewing by both eyes. Error bars represent the standard errors of the mean.

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close to the correct corner ("near", at the end of the short side of the rectangle) was also removed.

In both *landmark tests* there were no significant differences between experienced and non-experienced pigeons (Table 2, t-test, *near & distant landmarks test*: viewing with both eyes: t = 0.825, p = 0.422; viewing with the left eye: t = -1.317, p = 0.204; viewing with the right eye: t = 1.506, p = 0.153; *distant landmark only test*: viewing with both eyes: t = 0.779, p = 0.224; viewing with the left eye: t = -0.086, p = 0.933; viewing with the right eye: t = 0.904, p = 0.381).

In Fig 4 it has already been seen that the performance of both *landmark tests* was poorer in comparison to the other both tests. Both pigeon groups showed significantly more correct choices in the *cue conflict test* and the *geometry test* compared to the *near & distant landmarks test* and the *distant landmark only test* (RM ANOVA: experienced pigeons: F = 57.926, $p<0.001$; non-experienced pigeons: F = 27.603, $p<0.001$).

Table 2 also shows that most of the pecks were at the correct corner, followed by the diagonal corner (which had the same correct geometric information) and then the near and the distant corners.

Generally, both pigeon groups pecked the corner with the correct feature significantly more often in comparison to the other corners (FRM ANOVA on ranks, S4 Table), but the number of pecks to the various corners varied a lot. In detail, neither group differentiated significantly

Table 1. Correct choices (%) of experienced and non-experienced pigeons in all tests with all viewing conditions (mean±s.e.m.).

Test	Experienced pigeons (n = 10)	Non-experienced pigeons (n = 7)
Geometry test		
Binocular viewing	93.43±2.893	83.03±4.305
Viewing with the left eye	90.62±3.160	75.45±6.229
Viewing with the right eye	92.81±2.797	78.57±4.746
Cue conflict test		
Binocular viewing	91.25±4.340	93.75±2.893
Viewing with the left eye	88.13±3.892	91.07±2.499
Viewing with the right eye	87.19±4.356	90.18±2.305
Near&distant landmarks test		
Binocular viewing	46.56±3.437	50.89±3.900
Viewing with the left eye	47.19±2.207	42.86±2.334
Viewing with the right eye	42.81±3.549	50.00±2.552
Distant landmark only test		
Binocular viewing	42.81±4.168	47.39±4.376
Viewing with the left eye	38.44±2.874	38.02±4.068
Viewing with the right eye	39.06±4.147	44.79±4.320

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between the correct corner and the diagonal corner and the two corners that were directly neighboring to the correct corner and geometrically incorrect ("near" versus "distant"). This

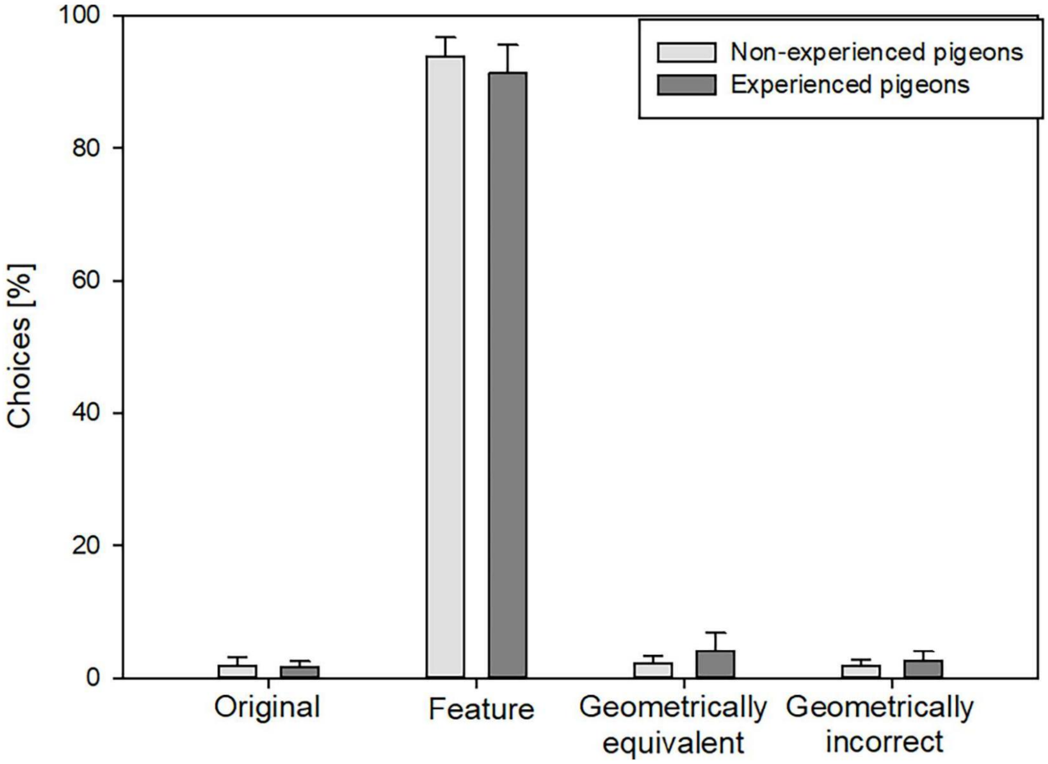

Fig 5. Percentages of choices to the various corners in the *cue conflict test* by non-experienced (n = 7) and experienced pigeons (n = 10) using both eyes. Error bars represent the standard errors of the mean.

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Table 2. Choices (%) of experienced and non-experienced pigeons in the *near & distant landmarks test* and the *distant landmark only test* (mean±s.e.m.).

Near&distant landmarks test		correct corner	diagonal corner	near corner	distant corner
Experienced pigeons	Binocular viewing	46.56±3.438	31.25±2.135	12.50±2.234	11.25±3.062
(n = 10)	Left eye	47.19±2.207	31.56±2.734	12.19±1.946	8.44±4.402
	Right eye	42.81±3.549	40.63±3.194	7.19±1.683	7.19±1.322
Non-experienced pigeons	Binocular viewing	50.89±3.900	33.04±3.039	9.82±3.006	8.48±1.767
(n = 7)	Left eye	42.86±2.334	36.61±3.900	12.05±2.499	8.48±6.115
	Right eye	50.00±2.552	32.14±2.950	12.95±4.494	8.48±2.788
Distant landmark only test		correct corner	diagonal corner	near corner	distant corner
Experienced pigeons	Binocular viewing	42.81±4.168	30.63±2.543	15.31±2.207	10.94±2.519
(n = 10)	Left eye	38.44±2.874	33.13±2.803	17.50±1.693	10.31±2.511
	Right eye	39.06±4.147	31.56±3.681	19.36±2.543	8.75±2.273
Non-experienced Pigeons	Binocular Viewing	47.40±4.376	33.33±3.194	13.02±0.960	6.77±3.168
(n = 7)	Left eye	38.02±4.068	31.77±2.726	22.92±2.234	6.77±1.491
	Right eye	44.79±4.320	28.65±2.604	16.15±3.064	7.81±0.699

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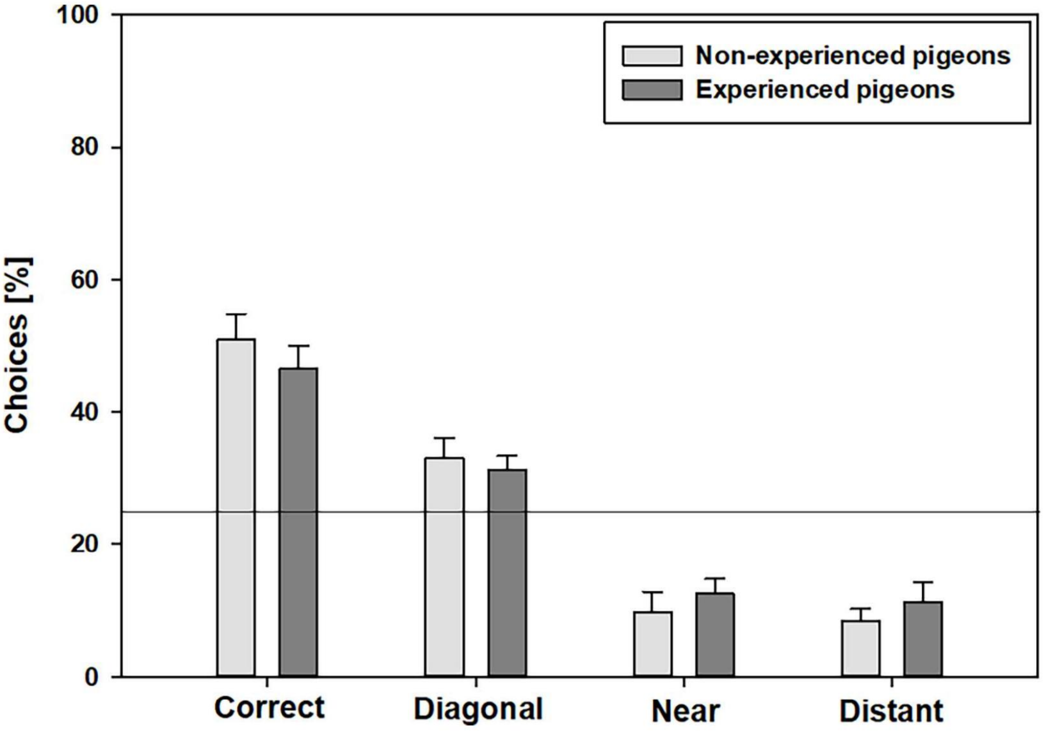

Fig 6. Percentages of choices to the various corners in the *near & distant landmarks test* by non-experienced (n = 7) and experienced pigeons (n = 10) using *both* eyes. Error bars represent the standard errors of the mean. The solid line at 25% indicates the probability of choosing the correct corner by random chance alone.

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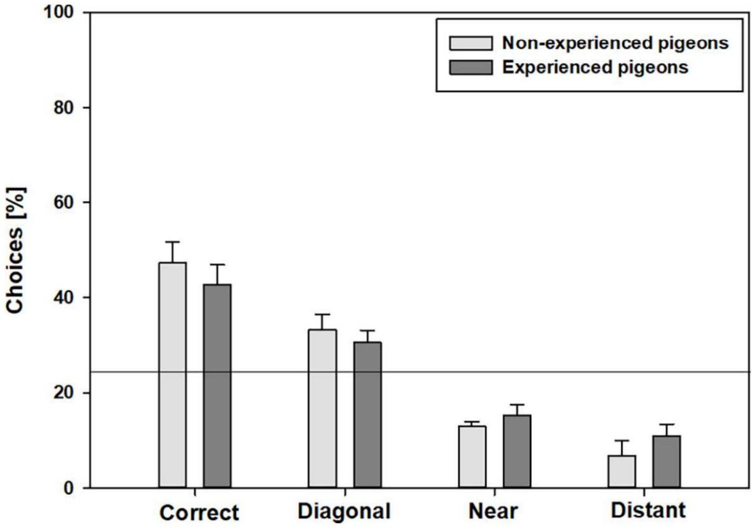

Fig 7. Percentages of choices to the various corners for the *distant landmark only test* by non-experienced (n = 7) and experienced pigeons (n = 10) using *both* eyes. Error bars represent the standard errors of the mean. The solid line at 25% indicates the probability of choosing the correct corner by random chance alone.

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was seen regardless of whether the pigeons used both eyes or just one eye (paired t-test, S5 Table, Fig 6).

The number of correct choices in the *near & distant landmarks test* was always significantly above 25% (the probability of choosing the correct corner by chance) regardless of whether the pigeons used both eyes or only one eye. But in both pigeon groups, the choice of the ***diagonal*** corner did not differ significantly from 25% (random chance), regardless of whether the pigeons used both eyes or just one eye (the number of the choice of the diagonal corner should be significantly under 25%) (S6 Table). Thus, we cannot exclude that the choice of this corner was by chance. Furthermore, the choice of the corner next to the correct one ("near", at the short end of the rectangle) did not differ significantly from 25% (random chance) if non-experienced pigeons used only their right eye (F = 7.19, p = 0.02).

In the *distant landmark only test*, only the feature that was adjacent but distant from the correct corner (at the end of the long side of the rectangle) was still shown. Again, both pigeon groups pecked the corner with the correct feature significantly more often in comparison to the other corners (FRM ANOVA on ranks, S7 Table), but the number of pecks to the various corners varied a lot. Like in the *near & distant landmark test* neither group differentiated significantly between the correct corner and the diagonal corner or the corners that were neighboring to the correct corner ("near" and "distant") regardless of whether the pigeons used both eyes or just one eye (paired t-test, Table 2, S8 Table, Fig 7). Additionally, non-experienced pigeons did not differ significantly between the correct and the near corner when using just one eye (Table 2, S8 Table, paired t-test, Fig 7).

In non-experienced pigeons, the choice of the correct corner was not significantly above 25% (random chance) if they used only their left eye (ANOVA/Fisher-test (LSD), F = 10.25, p = 0.009). So we cannot exclude that the choice of this corner was by chance. Furthermore, like in the *near & distant landmark test* in both pigeon groups, the choice of the diagonal corner was not significantly under 25% (random chance) regardless of whether the pigeons used both eyes or just one eye The choice of the corner next to the correct one ("near", at the short end of the rectangle) also did not differ significantly from 25% (random chance) if non-experienced pigeons used only their left or their right eye (left eye: F = 0.87, p = 0.373; right eye: F = 8.353, p = 0.016) or if experienced pigeons used only their right eye (F = 4.893, p = 0.04)

Discussion

The pigeons in this experiment differed in their navigational experience and learned to get food on the basis of information on a touch-screen monitor in an operant chamber. The stimulus was a schematic rectangular environment with landmarks in each corner, which were modified for different tests. Touch-screen experiments differ in several ways from open-field studies, e.g. the search area is relatively small and presented on a vertical display instead of a horizontal surface, and landmarks are not real 3-D objects but 2-D computer drawings, but therefore touch-screen experiments enable us to control variables more rigidly and easily and to conduct a larger number of trials. There are studies which show that at least the encoding of geometric information in chicks, like in children, is specifically based on subtle 3-D cues provided by the terrain instead of by salient 2-D brightness contours on surfaces or columns (chicks: [45]). Also studies with fishes show, that it is not the same whether animals have to orientate in a 2-D environment or in a real 3-D environment with extended surfaces and their properties [46,47]. Besides, the lack of disorientation procedures of the animals in 2D-experiments to avoid the use of inertial information could make comparisons with 3D-experiments difficult. However, there is no reason to underestimate that behaviors seen in an experiment with a touch-screen reflect general capabilities that would also be seen in the natural environment [48].

We found that non-experienced pigeons needed more time to habituate to the experimental situation and failed to do so more often. This could be due to their limited contact with novel situations and a higher stress level. Whereas experienced pigeons needed a similar number of days for pretraining and training, non-experienced pigeons needed significantly more days for training. It seems that experienced pigeons, which were familiar with combining a variety of different kinds of information during their flights, conjoin the relation between the response key and feature information already during pretraining. Perhaps in non-experienced pigeons this conjunction did not happen until the training phase. This might be an indication that experience (of any type) or the extent of exposure to environmental cues positively influences cognitive flexibility.

The *geometry test* (and also the *landmark tests*) showed that both pigeon groups were able to orientate on the basis of landmark and geometric information. In addition, the pigeons were able to conjoin landmark and geometric information, which is consistent with the results of Kelly et al. [4] and Kelly & Spetch [19]. They found e.g. that pigeons trained with features showed systematic rotational errors when the features were removed, indicating that they had indeed encoded geometry, even though this was not required to solve the task. We expected that navigational experience has an influence on encoding geometric information, but this was not verified in the frame of the present study. This is in contrast with findings in fishes, which showed that rearing conditions or rearing environment can alter the preferential use of geometric and landmark information [49] but is in line with findings in chicks. Several studies suggest, that the ability to deal with geometry seems to depend more on predisposed mechanisms than on rearing conditions and experience after hatching [11,50,51,52]. In chicks, the hippocampal formation seems to be recruited to support geometrical computations needed for goal orientation in a rectangular environment [53] and in another laboratory study, hippocampus-lesioned pigeons were insensitive to geometric information and relied exclusively on landmark information [26]. Following this, and the fact that pigeons with navigational experience have a larger hippocampus than pigeons without navigational experience [24], we expected a more distinct difference in encoding geometric information between the two groups. But it seems to be that, at least in a 2-D environment, the generally enlarged hippocampus of homing pigeons in contrast to other pigeon breeds and/or bird species [54] is sufficient for encoding geometric information.

The absence of hemispheric asymmetry (there were no differences between left-eye viewing and right-eye viewing) during the *geometry test* indicates that geometric information is encoded in both hemispheres. This is consistent with laboratory studies with homing pigeons [55] that showed that both hemispheres might be involved in encoding of geometric information, with the left hemisphere encoding absolute distance and the right hemisphere encoding relational geometry.

The *cue conflict test* placed geometric and landmark information in conflict, rather than removing the landmarks entirely. The *cue conflict test* showed that both pigeon groups preferred using landmark information, even if it was contradicted by correct geometric information. This is consistent with previous studies in chicks and fish [10,12,56] and one study in pigeons [55] but contrary to two others in pigeons [4,19]. Using a similar experimental design as we did, the study of Kelly & Spetch [19] showed that when geometry and landmarks provided conflicting information, pigeons divided their choices equally between the location defined by the correct landmark and the location defined by the correct geometry. One possibility for this discrepancy between their research and ours might be the breed of used birds: homing pigeons in our study versus Silver Kings in the Kelly et al. studies. Homing pigeons are selectively bred for accurate homing behavior, whereas, Silver Kings are typically bred for laboratory use or meat production and too large to fly long distances. Thus, it is not unlikely, that they not just differ in their homing behavior, but also in encoding geometric and featural information.

In the present study, landmark information overshadowed the geometric information even in the pigeons that had spent their whole life in the loft. Overshadowing (defined as the predominance of one kind of information over other kinds) is widely observed in the spatial domain, including in pigeons [57]. Our results indicate that this effect is not dependent on individual life history, at least in homing pigeons. Furthermore, neither group showed hemispheric asymmetry, which means that both hemispheres weight landmarks more relevant than geometry.

The *landmark tests* investigated whether the pigeons also use landmarks other than the landmark in the correct corner for orientation. Both pigeon groups demonstrated in principle, the ability to also use distant features to correctly locate the rewarded corner and chose the correct corner significantly more often than the other corners, but performance was much worse in comparison to the other tests. This is consistent with a previous study on pigeons [19] but contrasts with studies on chicks [10] and rats [7] which showed that these species have failed to show learning of the features in the geometrically incorrect corners. A plausible explanation may be the inhabitation of contrasting ecological niches. The lack of differences between experienced and non-experienced pigeons indicates that encoding landmark information is not dependent on experience of navigating long distance over extended landscapes. Interestingly, the differentiation between the various corners was difficult. The number of choices between the correct and the diagonal and the near and the distant feature did not differ significantly and in the *distant landmark only test* non-experienced pigeons even had problems with the differentiation of the correct corner and near corner if they used just the left or right eye. It looks very much that either the pigeons could not use landmark and geometry information together, or that the conjunction of several features is important for orientation, with each landmark being a crucial element, the absence of which will result in poorer orientation performance.

The second interpretation also explain the fact that the choice of the different corners often does not significantly exceed the 25% level of random chance. This is also consistent with the results of the *cue conflict test*, which demonstrated the pigeons' preference for landmarks. Non-experienced pigeons had more problems with the differentiation of the various corners and this might be an indication that experience or the extent of exposure to environmental cues positively influences the capability to conjunct several features for orientation.

We found hemispheric asymmetries particularly in non-experienced pigeons in both *landmark tests*. In non-experienced pigeons the differentiation between the various corners was worse under monocular occlusion. This was already seen in the comparison with the probability of choosing the correct corner by chance (25% or 50%). In the *distant landmark only test* this was even more distinct, but without a clear superiority for one eye respectively one brain hemisphere. It seems that the viewing condition became more important for non-experienced pigeons when less featural information (especially features) was available. Or, vice versa, the degree of experience became more important when less featural information was available. Many studies about avian brain lateralization are based on chicks, and it is known that there are differences between chick and pigeons not only in regards to brain morphology in general but also specifically for lateralization [23,56,58]. This might not be too surprising, since chickens and pigeons develop differently (altricial vs. precocial) and also show profound differences in the use of space under natural conditions (ground living vs. flying over long distances). It has been suggested that chicks process spatial information primarily in the right hemisphere [59,60]. In contrast, several studies on pigeons have shown a left-hemispheric superiority for navigation and/or discrimination of various visual objects [15,41,61]. Thus, it should be expected that test performance would be better with the right eye than with the left, but our study did not support that. Generally, we cannot constitute a clear hemispheric superiority, but there were differences between the differentiation of the various corners in both landmark tests using both eyes or just one eye. The organization of processing spatial information in the left or right hemisphere seems to be more diverse and it is difficult to generalize which kind of information will be processed in which hemisphere. That diversity is supported here by the different results of the both *landmark tests* under monocular occlusion.

That there is a high diversity in the organization of processing spatial information in the different hemispheres was also the assumption of Wilzeck et al. [54]. On the one hand, the authors also showed a pattern for the hemispheric encoding of geometric and landmark information by the pigeon that was different than the pattern previously reported for the domestic chick. On the other hand, they showed that the relative use of geometry and landmarks depended on experience. However, this referred to different experiences acquired by the pigeons during different conditions in a kind of pretraining (where there was just geometric information available or geometric and landmark information available) and thus was not directly comparable with the kind of experience of the pigeons in the present study. But the authors found an experience-dependent effect, and that is consistent with the role of experience in the present study.

Generally, results with chicks have shown clear differences in spatial processing (encoding relational spatial information and absolute metric information) between left-hemispheric and right-hemispheric use as well as little differences between right-hemispheric and binocular use [62]. Yet pigeons in the study of Wilzeck et al. [54] showed virtually no difference between left-hemispheric and right-hemispheric use (and no distinct left-hemispheric dominance) but did show a difference between the binocular condition and each of the monocular conditions [54]. That was just in part shown in both *landmark tests* of the present study. Differences between binocular and monocular viewing were observed only in the *landmark tests* and here particularly in non-experienced pigeons. Thus, the *landmark tests* showed that the condition of binocular or monocular viewing could have, after all, an influence on encoding geometric or landmark information. Those tests also showed that encoding is influenced by experience, because the choice of the four various corners differed between experienced and non-experienced pigeons and the different viewing conditions, but without a clear tendency to one hemisphere. A stronger representation of visual stimuli in the pigeons' left hemisphere, which was reported in earlier studies in various laboratory settings [38,41,61,63], could not be confirmed. We expected that at least experienced pigeons would be able to differentiate better between the four various corners if they could use their right eye and thus, their left hemisphere. But that was not the case. Perhaps more realistic experiments in a 3-D environment, or even free-flight experiments, could provide more insight about this phenomenon. Also repeated discrimination tasks might be able to help clarify this, because Verhaal et al. [64] has shown that differential left-right performance is already present before learning but increases substantially as soon as some cues are associated with a reward. The results of the present study support the conclusion that each hemisphere of the pigeon brain encodes multiple cues that may allow the bird to process orientation tasks in a fast and flexible manner.

In conclusion we can say that, in a 2-D-environment, pigeons are able to encode geometric and landmark information for orientation but prefer using landmark information. In the present study, there is no influence of navigational experience on encoding geometric and landmark information. Encoding geometric or featural information cannot be assigned to the left or right hemisphere. Either it is processed in both brain hemispheres, or, in case of processing geometric information in one hemisphere and landmark information in the other, both processes are integrated before response. More investigations are necessary to clarify these open questions. The conjunction of geometric and landmark information is important for orientation, probably processed in both hemispheres and influenced by navigational experience.

Supporting information

S1 Table. Statistical results of comparisons between the choices of the correct corners and the probability of choosing the corner by chance (50%) in the *geometry test* (ANOVA/Fisher's least significance difference test (LSD)).
(DOCX)

S2 Table. Statistical results of comparisons between the choice of the correct feature and the other corners (FRM ANOVA on ranks) in the *cue conflict test*.
(DOCX)

S3 Table. Statistical results of comparisons between the choices of the correct landmark and the probability of choosing the corner by chance (25%) in the *cue conflict test* (ANOVA/ Fisher's least significance difference test (LSD)).
(DOCX)

S4 Table. Statistical results of comparisons between the choice of the correct feature and the other corners (FRM ANOVA on ranks) in the *near & distant landmarks test*.
(DOCX)

S5 Table. Statistical results of comparisons between the choices of the various corners in the *near & distant landmarks test* (paired t-test).
(DOCX)

S6 Table. Statistical results of comparisons between the choices of the *diagonal* corner and the probability of choosing the corner by chance (25%) in the *landmarks test near & distant* and the *distant landmark only test* (ANOVA/ Fisher's least significance difference test

(LSD)).
(DOCX)

S7 Table. Statistical results of comparisons between the choice of the correct feature and the other corners (FRM ANOVA on ranks) in the *distant landmark only test*.
(DOCX)

S8 Table. Statistical results of comparisons between the choices of the various corners in the *distant landmark only test* (paired t-test).
(DOCX)

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RESEARCH ARTICLE

The Influence of Social Parameters on the Homing Behavior of Pigeons

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Abstract

Homing pigeons develop preferred routes when released alone several times from the same site, but they sometimes diverge from their preferred route when subsequently released with another pigeon. Additionally, group flights show a better homing performance than solo flights. But this knowledge is based on studies involving both sexes and lacks analyses of social parameters such as mating or breeding status, even though it is known that such parameters have an influence on behavior and on motivation for specific behavioral patterns. GPS trackers were used to track 24 homing pigeons (9 breeding pairs and 6 unmated females) as they performed a familiar 10km route in various pair and group combinations. Comparisons of efficiency indices (quotient between straight-line distance and pigeon's track) reveal that unmated females show the best efficiency in single flights. Generally, group flights show the best efficiency followed by pair flights with a social partner of the opposite sex. Pair flights with the mated partner exhibit the poorest performance. Additionally, just before squabs hatching, females show a higher efficiency index when released at 8 am, compared to releases at 2 pm. Our results indicate that homing flight efficiency can provide insight into individual motivation and that social parameters have an influence on homing performance on a familiar route.

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Introduction

Homing pigeons are well-known for their excellent homing abilities, and the mechanisms they use to navigate homeward from distant release sites have been well studied. Several orientation cues and mechanisms e.g. olfactory cues, visual landmarks, sun compass, and magnetic compass are known to be involved in homing behavior, and parameters such as motivation and experience are also known to be important for fast and successful homing [1–6].

In recent years, the number of publications on homing tracks or pathways used by homing pigeons has greatly increased, which is due in large part to the advent of micro-global positioning system (GPS) data loggers that can be attached to a pigeon's back, thereby enabling detailed analysis of flight trajectories [7,8]. The preferred routes of homing pigeons are rarely efficient straight lines, and there are differences between homing tracks from unfamiliar release sites and familiar release sites [9]. It is not entirely clear what makes a route from familiar sites preferred by pigeons, but Lipp et al. [10] have suggested that at least railway tracks and highways were used for following on the way home from familiar release sites. Yet there are regional differences, and this phenomenon is not observed in all pigeons [11, 12]. The fact is that homing pigeons develop individual preferred routes when released alone several times from the same site [13]. It must be considered that pigeons live in social groups, usually as monogamous pairs, and prefer to home in the company of other pigeons [14]. Thus, the presence or absence of conspecifics could influence the homing track and homing speed. If two pigeons with different preferred homing routes from the same familiar site are released together from that site, they come into conflict what to do. If the difference between two birds' directional preferences is small, they average their routes, but if the difference surpass a critical threshold, either the pair splits apart or one of the two birds become the leader [15]. Several research groups have also shown that the homing performance of two or more birds was more efficient than the homing of either one, even when single performance of individual birds was poorer [15, 16, 17].

All this knowledge about the homing tracks used is mostly generalized for both sexes, males and females, and does not include social parameters such as mating or breeding status. Homing pigeons live in flocks with a flexible social structure, not a strict hierarchy. They live in monogamous pairs and usually mate for life. They have fixed territories centered on a nest and males show strongly territorial behavior, but both birds of a well-bonded pair will defend the nest territory. Sometimes, particularly dominant males try to mate with more than one female. Males and females both engage in breeding and the manner in which the sexes share incubation is ritualized. Males sit from mid-morning (approximately 10 am) to late afternoon (approximately 5 pm), females from late afternoon to mid-morning the next day [18]. Pigeon fanciers have used these particularities of behavior to develop differential strategies aimed at improving the motivation to home when displaced and the homing performance during competition. One strategy is that they allow the pigeons to mate and to build a nest, but then they separate at least one partner from the nest for a few days. After returning from a race, these pigeons are now allowed to go directly to their waiting partner and nest. Another, apparently successful, method is to bring a possible competitor into the loft just before catching the pigeons for a race. This motivates the pigeons to hurry home [19].

This anecdotal knowledge and the high number of studies of homing tracks without any analysis of social parameters leads to the question of what ways parameters such as sex, mating status, and/or breeding status influence the homing performance or the motivation to fly home. It is better to analyze homing tracks for a familiar route, because it makes the performance mostly independent of the individual pigeon's navigational ability. If every pigeon knows the way home, any differences in homing performance should be due to other reasons. Biro et al. [15] have provided an experimental design for this. They analysed the homing tracks of solo and dual flights on a familiar route. In our study we also used high-resolution GPS loggers and adopted Biro's et al [15] experimental design as far as possible. But we put our focus on how social parameters such as sex, mating status, and breeding status might influence homing performing a familiar route. We anticipated that mating and/or incubation functions as a motivational factor for homing performance. Additionally, we made group flights to investigate whether flying in groups also increased performance.

Materials and Methods

Ethics Statements

All applicable international, national, and/or institutional guidelines for the care and use of animals were followed. The study was approved by the Committee on the Ethics of Animal Experiments of North Rhine-Westphalia (Ref. 84–02.04.2011.A137).

Study Setting

Nine well-established pairs of homing pigeons (*Columba livia* f.d., 9 males and 9 females) and six unmated females (unmated males were not available) from the neighboring loft were selected as subjects. The two lofts were separated from each other by just a small corridor, and both lofts were constructed and equipped in the same way. All the pigeons were at least one year old and successful homers over distances up to 300 kilometers. Males and females of mated pairs were separated for several weeks and brought together just shortly before the beginning of the tests in order to synchronize their breeding cycles. They were allowed to lay eggs and to breed (to ensure that mating succeeded). Food and water was available ad libitum. All pigeons were housed in the pigeon lofts of the University of Düsseldorf, with breeding boxes and seating-accommodations inside. The experiments were carried out during the summertime (August-September). The weather was always sunny or moderately cloudy with temperatures between 17–24°C. The wind speed and wind directions according to the "German Weather Service" can be seen in the supporting information, S1 Table. Releases were done before the beginning of main molting. The pigeons of both groups had just changed a few of their primary feathers.

All pigeons were fitted with a Velcro strip, attached to their back with leather glue applied to trimmed feathers, and they were trained to carry plexiglas dummies (weight: 18 g). Each bird was then released alone from the same release site 8 times consecutively, with one release per day (straight-line distance ~10 km, flight direction south-southeast). All mated females had laid their eggs by the end of this training period. After that, the pigeons were tagged with GPS loggers (12g; Technosmart; Rome, Italy) for each flight and had to fly the same route again for 6 times, consecutively once per day. GPS loggers (see [7] for technical description) were also attached to the pigeons' backs by the Velcro strips. All releases were carried out from release boxes which had an exit on one side and permitted a view of the sky. By the end of this training phase, we assumed that the pigeons were quite familiar with this release site and the way home.

Having completed these solo flights, the pigeons were assigned to different pair and group combinations and released from the same site simultaneously with their flight partner(s). Mated pigeons had to fly first with their mated partner (I) and then with a fellow of the opposite sex that was not their own mating partner (II). In the next release, pigeons had to fly with a pigeon of the same sex (III). Subsequently, we released groups of six pigeons consisting of 3 mated pairs (IV). The unmated females also carried out the three flights in pairs, matched up with one another and all six unmated females were released together for the group flight. As in [15], birds were given one or two solo flights after each paired release, in order to remember their own preferred route. Each flight unit (solo pigeon, duo, or group) was not released until the previous flight unit was no longer visible to the researcher and a minimum of 10 minutes had elapsed. The last releases were group flights with all 9 mated males together or all 9 mated females together. While previous releases were randomly assigned during the day, these final flights in groups of 9 had release times of 8am and 2pm. Each group made one flight at 8 am and one flight at 2 pm. The reason for choosing these release times was that males and females have different, fixed times of the day for their shift sitting on the eggs, as mentioned above. The male sits on the nest from approximately 10am to 5pm; whereas, the female sits on the nest for the rest of the time. Thus, at 8 am, the females should be on the nest, and at 2 pm, the males should be there. These last releases took place approximately 17 days after egg laying. Since pigeons have a breeding period of approximately 18 days, the squabs would be hatching quite soon. We assumed that this anticipated parenting could increase their motivation for efficient homing flight.

The constellation of duo and group flights was randomized. To prevent any influence of different weather conditions or environmental effects, we disclaimed randomizing the order of pair and group flights.

Time-stamped positional fixes were logged every second and were downloaded upon recovery of the device. The positional data were superimposed onto Google Maps using Habitat Tracker software (Biobserve; St. Augustin, Germany). To minimize observer bias, blinded methods were used whenever behavioral data was recorded. Random numbers were assigned to each pigeon, in order to prevent the analyst from knowing which data set belonged to which pigeon until the end of the analysis.

Data Analysis

For each flight, track length was calculated as the total distance travelled to reach home (the sum of the distances separating all consecutive points of a track). Calculating track length started promptly after releasing and ended once the pigeon reached the university building with the home loft. An efficiency index was calculated as the straight-line distance between the release site and home, divided by the individual track length. Since an efficiency index of 1 would mean that the pigeon flew a straight-line, values close to 1 show a high homing efficiency. We used the efficiency index and not the homing time or homing speed for analysis because homing time depends in part on the physical strength (and thus the flight velocity) of the individual pigeons, which was of no interest in this study on the directness of the flight route. To prove this argument, we compared at first body weights of male and female pigeons statistically by t test. To exclude a correlation between wind speed/wind direction and homing efficiency, Pearson Product Moment Correlations were carried out. Nevertheless, averaged homing speed values for each track (straight-line distance divided by the homing time) were also provided and some calculations were also carried out with them.

Efficiency indices were compared statistically by t test, Mann-Whitney test (in case of non-normal distribution), ANOVA (on ranks), or Friedman Repeated Measures Analysis of Variance on Ranks (FRM ANOVA on ranks) in case of comparisons between the sexes. Comparisons within the sexes were done with parametric and non-parametric tests for dependent data, namely the paired t test and Wilcoxon Signed Rank test. The level of significance was 5%. SigmaPlot/SigmaStat version 12.0 was used for all statistical calculations.

Results

We first compared body weights of males and females and noticed that there were significant differences between them with a physical superiority for the males (498.148 g ± 49.54 vs 461.500 g ± 63.97; t test, $t = 2.215$, $p = 0.032$). There were no significant correlations between the homing efficiency and the wind speed (Pearson Product Moment Correlation, $r = 0.335$, $p = 0.344$) or wind direction ($r = -0.555$, $p = 0.096$). This is the same between homing speed and wind speed ($r = 0.227$, $p = 0.529$) or wind direction ($r = -0.363$, $p = 0.303$).

After this we examined the development of homing routes during repeated solo flights from the same release site. All pigeons improved their efficiency during these flights. Individual efficiency index increased significantly in the first five days of training with GPS loggers (FRM ANOVA on ranks, Chi-square = 21.567, $p<0.001$; Table 1). After that, the efficiency stagnated or even decreased. This was the same after analyzing speed values (FRM ANOVA on ranks, Chi-square = 42.567, $p<0.001$; Table 1) what makes it likely, that both parameter, efficiency index and homing speed, would give similar results. Because of the found differences between body sizes of the sexes, we kept the use of efficiency indices and carried out the following analysis just with them.

Table 1. Efficiency indices and speed of all pigeons for solo flights with GPS-loggers (mean ± sd).

	Efficiency index (n = 24 per day)	Speed (km/h, n = 24 per day)
Day 1	0.784±0.107	53.410±7.183
Day 2	0.815±0.131	61.239±7.327
Day 3	0.852±0.096	61.573±7.688
Day 4	0.870±0.075	62.597±5.669
Day 5	0.899±0.057	70.300±9.185
Day 6	0.870±0.0469	53.930±7.047
Day 7	Duo flight I	Duo flight I
Day 8	0.790±0.0198	53.917±7.047
Day 9	Duo flight II	Duo flight II
Day 10	0.865±0.0846	63.600±9.345
Day 11	Duo flight III	Duo flight III
Day 12	0.828±0.116	72.548±13.809
Day 13	Group flights	Group flights

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Next we analyzed solo flights of our three groups of pigeons (Table 2). For statistical comparison, we used the efficiencies of all solo flights: the six ones before the beginning of the pair and group flights and the single flights between them. Here we noticed that there were significant differences between the three groups (ANOVA on ranks, H = 8.421, p = 0.015, Table 2). Unmated females had the highest efficiency in single flights (0.860±0.103, mean±sd), followed by the mated males (0.831±0.104). Mated females had the poorest efficiency (0.815±0.104). Mated females also flew slower (58.358±10.022) than both other groups (mated males: 60.649 ±11.038; unmated females: 62.743±8.590), but not significantly so (ANOVA on ranks, H = 5.937, p = 0.051, Table 2). Fig 1 illustrates an example of GPS tracks obtained from an unmated female.

No pigeon stopped on their way home in any of the solo, duo or group flights. Besides, the pigeons never split apart in any of the duo or group flights; they always remained together. No circling over the releasing site could be observed. A comparison of the solo, duo, and group flights of unmated females shows that efficiency increases with group size in a significant way

Table 2. Efficiency indices and homing speed of all flights of all pigeons (mean ± sd).

	Efficiency	Speed (km/h)
Solo flights–unmated females	0.860±0.102	62.743±8.590
Solo flights–males	0.831±0.104	60.649±11.038
Solo flights–mated females	0.815±0.104	58.358±10.022
Duo flights:		
Mated pairs	0.795±0.044	64.884±6.586
Duos of same sex–unmated females	0.891±0.070	70.958±11.570
Duos of same sex–males	0.803±0.095	56.703±6.963
Duos of same sex–females	0.827±0.037	58.434±5.097
Duos of opposite sex	0.910±0.023	81.956±5.292
Group flights (unmated females)	0.956±0.009	91.534±1.842
Group flights (mated pairs)	0.949±0.018	91.278±3.3655

See the main text and Table 3 for statistical results. (The means for solo flights are calculated from all solo flights).

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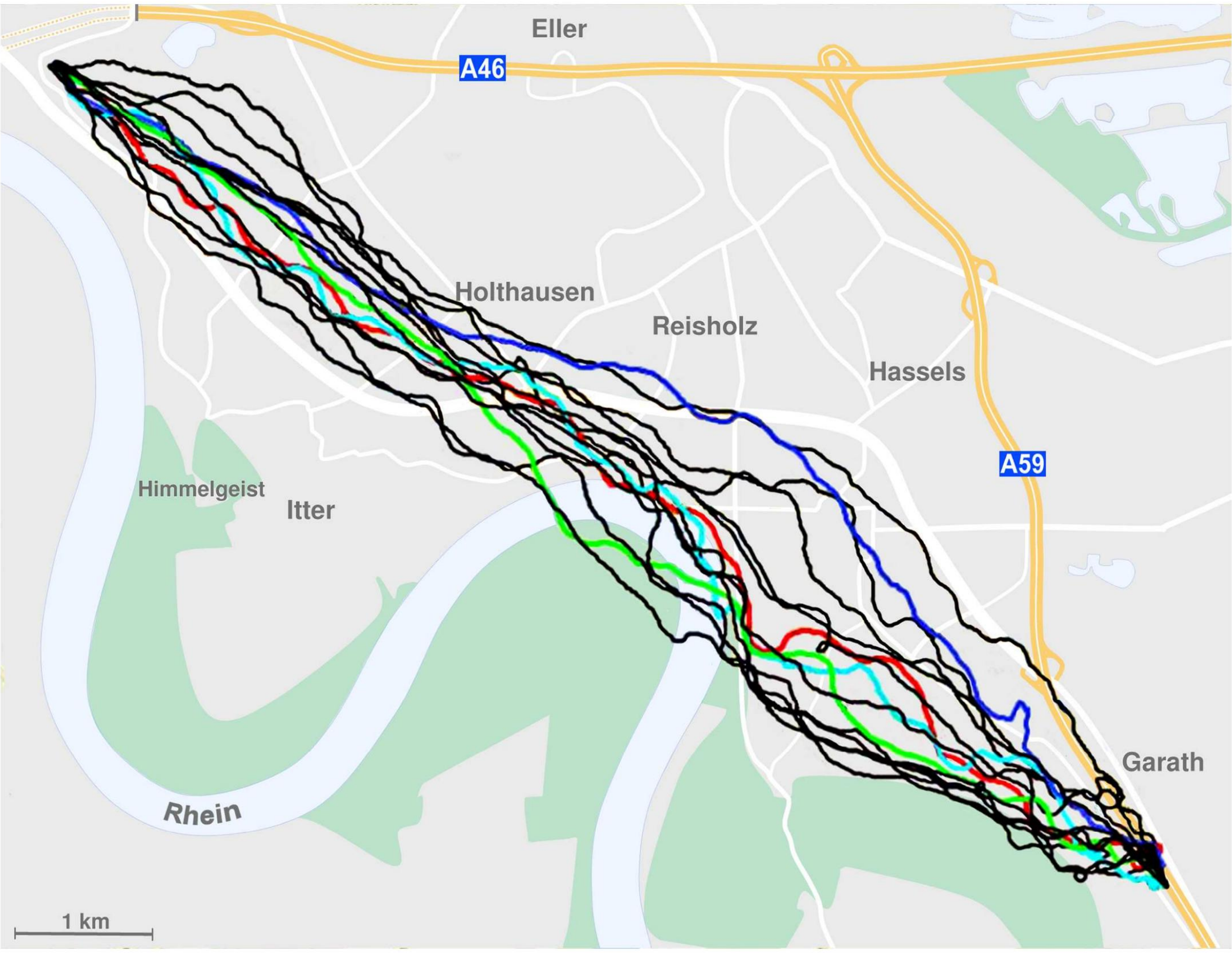

Fig 1. Map showing all solo, duo, and group flights of an unmated female. Black = solo flights; red, blue, green = 1st, 2nd, and 3rd duo flights; light blue = group flight.

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(ANOVA on ranks, H = 9.420, p = 0.009; Fig 2). The group flight (consisting of all six unmated females) showed the highest efficiency (0.956±0.009) followed by duo flights with another unmated female (mean efficiency index: 0.891±0.070). Single flights showed the poorest efficiency (0.860±0.103).

Fig 3 and Tables 2 and 3 summarize the results of the mated pigeons; Table 2 also provides an overview of homing speed. In combination I ("mated pairs", Fig 3) and the group flights ("group of six", Fig 3) males and females are presented with one vertical bar because they always flew together and therefore always had the same efficiency. There was a statistically significant difference between the different flight combinations (ANOVA on ranks, H = 51.452, $p<0.001$). Both sexes showed the lowest efficiency in duo flights with their partner (0.795 ±0.044) and the highest efficiency in group flights with two more pairs (0.949±0.018). The efficiency index of the group flight was always significantly higher than the efficiency index of solo or duo flights (see Table 3). Duo flights with a social partner of the opposite sex showed a

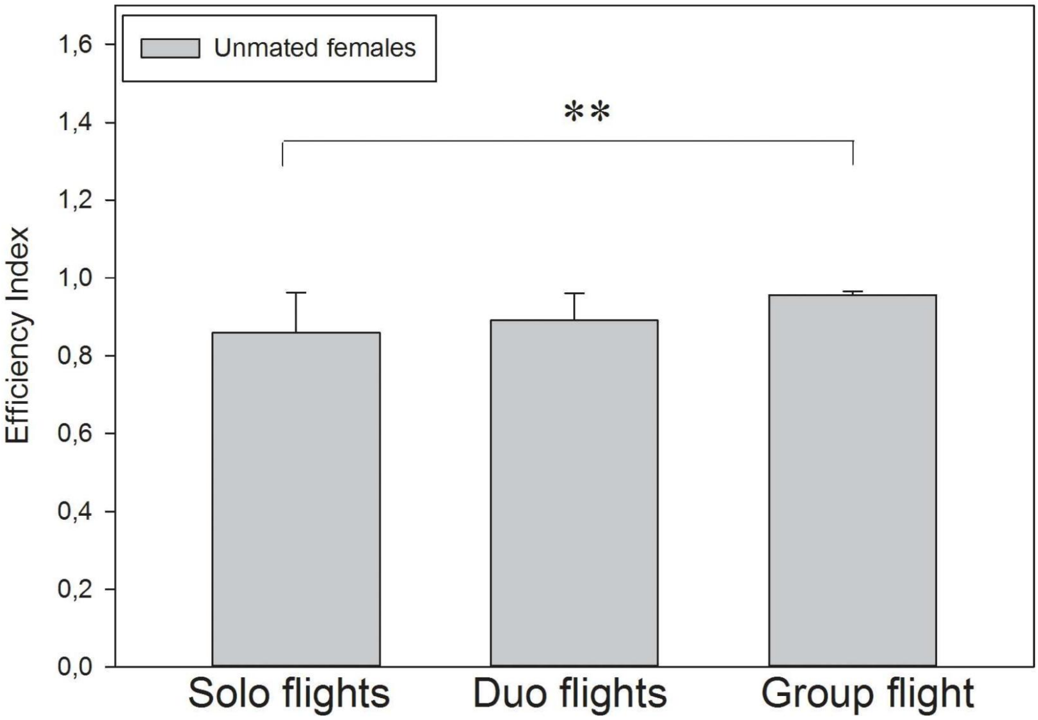

Fig 2. Efficiency indices (mean ± sd) of unmated females in solo, duo, and group flights (p = 0.009).**

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significantly higher efficiency than duo flights with a social partner of same sex (paired t test, males: t = 3.184, p = 0.013; females: t = -7.552 p<0.001) or the mated partner (paired t test, males: t = 6.457, p<0.001; females: t = 7.526, p<0.001). Females also showed a significantly higher efficiency index in duo flights with a social partner of the opposite sex than in solo flights (Mann Whitney test, T = 531.50, p = 0.002).

The results of the releases at different times of the day are shown in Fig 4. Mated females showed a significant higher efficiency at 8 am than at 2 pm (0.914±0.013 vs. 0.881±0.004; Wilcoxon Signed Rank test, T = 43,000, p = 0.008) and in comparison to the mated males at 8 am (0.888±0.012; Wilcoxon Signed Rank test, T = -36,000, p = 0.008). Mated males did not show a significant difference between 8 am and 2 pm (0.888±0.012 vs. 0.890±0.021; Wilcoxon Signed Rank test, T = 15,000, p = 0.426) or in comparison to mated females at 2 pm (0.890±0.021 vs. 0.881±0.004, Wilcoxon Signed Rank test, T = 20,000, p = 0.195).

Discussion

In this study we examined the influence of social parameters such as sex, mating status, or breeding status on homing performance for a familiar route in homing pigeons. After training the pigeons to a release site approximately 10km from their home loft, we released them in various duo and group constellations, to assess the social parameters mentioned. Due to repeated releases and the fact that the distance between the release site and the home loft was not very long, the pigeons became more and more familiar with this route, and very probably knew the most efficient route. The initial solo flights showed an increase in efficiency during the first days and then stagnation. Thus, we assume that training or learning would not have had any further influence on subsequent flights and that differences in the efficiency index were due to differences in motivation. Of course, group size can also improve efficiency, and generally it is

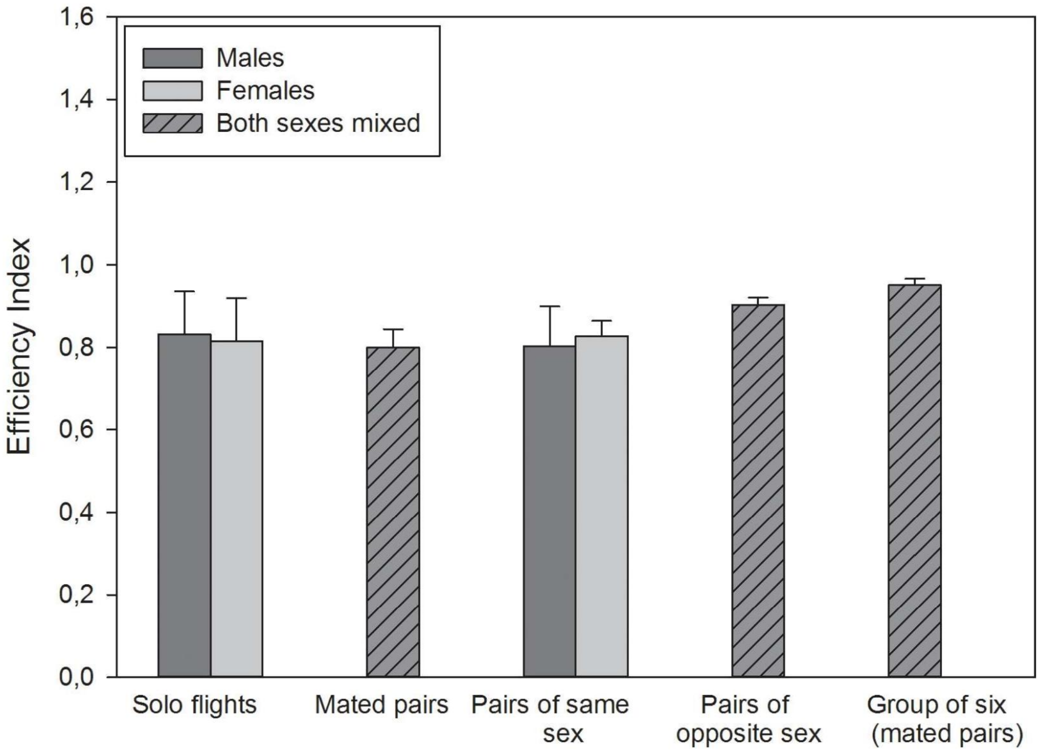

Fig 3. Efficiency indices (mean ± sd) of mated males and females in solo, duo, and group flights. See the main text and Table 3 for statistical results.

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difficult to distinguish between the ability to fly home and the motivation to make use of it, but it seems to be most probable that motivation influences efficiency index of a familiar route in a strong way.

Table 3. Statistical results of comparisons between efficiency indices of solo, duo, and group flights (n.s.: p>0.05).

	Solo flights -males-	**Solo flights -females-**	**Duo flight I -males-**	**Duo flight I -females-**	**Duo flight II -males-**	**Duo flight II -females-**	**Duo flight III -males-**	**Duo flight III -females-**	**Group flights**
Solo flights -males-	/	n.s.	n.s.	T = 252.00, p = 0.032	n.s.	n.s.	n.s.	T = 493.0, p = 0.007	T = 1096.5, p<0.001
Solo flights -females-		/	n.s.	n.s.	n.s.	T = 531.5, p = 0.002	T = 347.0, p = 0.030	n.s.	T = 1146.0, p<0.001
Duo flight I -males-			/	/	t = 6.457, p<0.001	t = -6.547, p<0.001	n.s.	n.s.	t = 8.353, p<0.001
Duo flight I -females-				/	T = 45.00, p<0.001	t = 7.526, p<0.001	n.s.	n.s.	t = -9.658, p<0.001
Duo flight II -males-					/	n.s.	t = 3.184, p = 0.013	t = -3.070, p = 0.008	t = -5.622, p<0.001
Duo flight II -females-						/	t = 4.000, p = 0.001	t = -7.552, p<0.001	n.s.
Duo flight III -males-							/	n.s.	Z = -2.668, p = 0.004
Duo flight III -females-								/	Z = 2.692, p = 0.004

Duo flight I: mated pairs; Duo flight II: pairs of opposite sex; Duo flight III: pairs of same sex; Group flights: three mated pairs.

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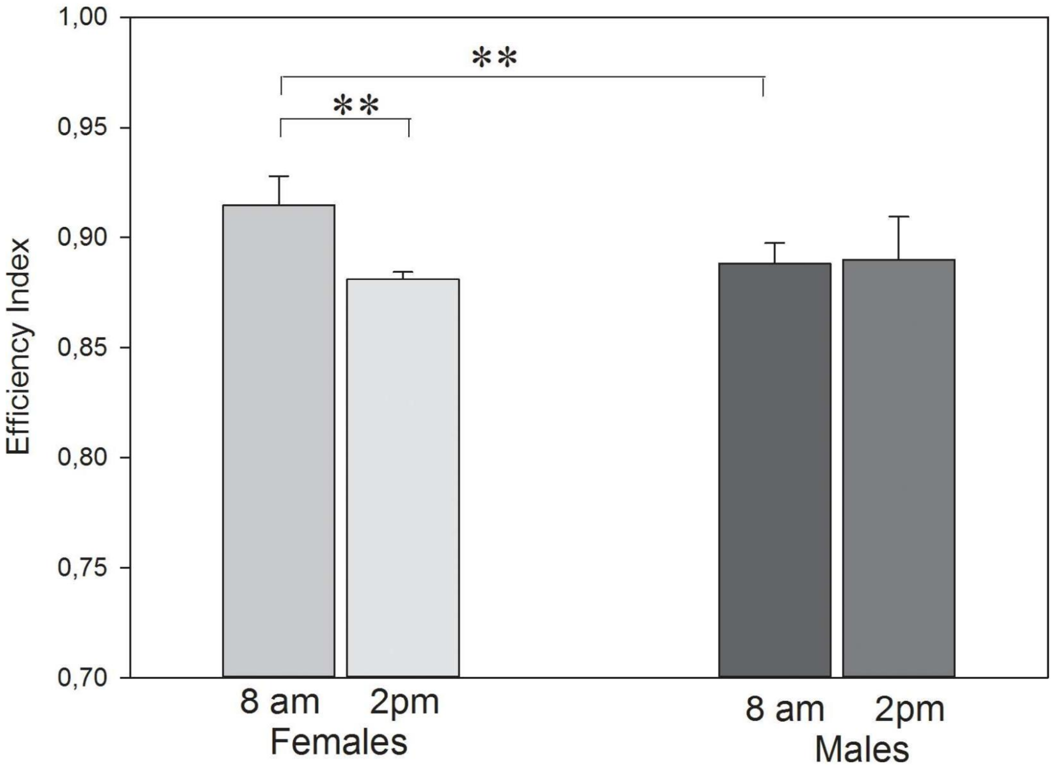

Fig 4. Efficiency indices (mean ± sd) of mated females and males at various times of the day (p = 0.008).**

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We first showed that efficiency increased during the first five days of training with GPS loggers. On day six and in the single flights between the pair and group flights, efficiency stagnated or even decreased slightly. This is consistent with the findings of Guilford & Biro [9] who observed a gradual development of route performance with decreasing effects after a rapid initial improvement. This is also characteristic of learning processes in general.

Our data also confirms the results of several other research groups [13, 15, 20, 21] that repeated releases improve homing performance. Pigeons typically reach a high level of route efficiency within approximately eight to ten flights [13]. Apparently we observed a learning process whereby the birds were adopting the most efficient route home, which of course means an increasing approximation to the straight-line.

Generally, mean efficiency index of solo flights was similar to those described in the literature, where the values vary between 0.66 and 0.91, but mostly are around 0.83 (summarized in [9]). Theoretically, efficiencies seem to allow room for some improvement. Wiltschko et al. [12] discussed this point and suggested a certain increase in efficiencies with increasing distance. They assumed that the shortness of the distance (and a 10 km straight-line distance as in our study is in fact short for a homing pigeon) may not present a real challenge for the pigeons, so they may not have felt a need for further improvement. Our observed range between efficiencies supports our hypothesis that the efficiency index over a (relatively short) familiar route can be influenced by the social setting or the type of social relations to flight companions. Only a few studies have dealt directly with the possible influences of birds' motivation on homing performance [22, 23].

Interestingly, unmated females showed a better efficiency index in both, solo flights and duo flights than the mated females or males. It seems to be that celibacy is not just a motivational factor for homing performance but even a strong one. The higher efficiency index of the unmated pigeons' group flights is consistent with the findings of Biro et al. [15] and Dell'Arriccia et al. [16] which showed that group flights generally show a better homing performance than solo flights, even if the solo performance of the individual birds was poorer. Several research groups have described this phenomenon and explained it with the "many-wrongs" principle and other models of group navigation that predict the cancelling of individual navigational errors [15, 16, 24, 25]. By contrast, Santos et al. [26] showed that the circling time increases with group size because of establishing a leader. We did not observe this in our duo and group flights, and in our opinion, one must distinguish between the initial circling and the final chosen route, which represents the efficiency index. The efficiency index of mated pigeons' group flights was higher as in solo or duo flights. Thus, group size has an effect on efficiency that is distinct from motivational effects. The speed values showed similar tendencies, but their interpretation is more difficult because we cannot estimate the influence of physical fitness in case of divergences (see above).

It is assumed that pigeons released alone show extended circling time at the release site because they search for other pigeons; whereas, duos and small flocks usually leave the release site much faster and more directly [27]. Thus, it must be expected that duo or group flights show a higher efficiency index than solo flights because of a socially motivated behavior at release site. This is consistent with our findings for the unmated females but not for the mated pigeons. Interestingly, the motivation to fly home via the most direct route is poorest if mated pairs fly together. Apparently, flying with the mated partner reduces motivation to go home, and thus the efficiency index, because staying with the mated partner is the motivational factor and acts as a reward. This is consistent with common treatments of pigeon fanciers who know that the mated partner in combination with the breeding place leads to a very high motivation in pigeons and can be used to improve homing performance. So usually just one pigeon from the couple participates in a pigeon race while the other one waits in the loft [19].

It would be interesting to test whether the phenomenon of poorer performance in (mated) pair flights disappears when flying longer distances or in flights from unfamiliar release sites, since these kinds of flights would be a bigger challenge for their navigational capability and it is possible that now non-navigational parameters become more dispensable. As mentioned above, the efficiency index increased significantly in group flights where three mated pairs were released together. There is always a tendency to travel in groups (even in flying a familiar route), and it has been shown that the nature of social relationships within the group can have an influence on the choice of route [28]. In our study, the good homing performance in all groups indicates that group flights are more efficient in general and not strongly influenced by sex, mating, or incubation.

Our last releases showed that breeding or incubation status is a motivational factor, but these differences are significant only in females, which seems to suggest that female pigeons attach greater importance to the behavior of sitting on eggs, perhaps because of their larger investment (they lay the eggs and have longer turns of breeding) [29]. Wallraff [6] showed that homing performance exhibits a clear annual periodicity (at least in birds released at unfamiliar locations), but he did not find a correlation between the breeding cycle and homing performance, maybe because domestic pigeons breed basically all year if e.g. food availability is guaranteed. Our results show that there is a correlation between the breeding status and the efficiency index. An existent clutch or an upcoming eclosion increases motivation to home, at least in females and at least in performing a short distance from a familiar site. This is consistent with the findings of Clausen et al. [22] who showed that the breeding cycle has an influence on homing (speed). In their study, the pigeons showed an increase of homing performance during incubation with a peak at eclosion time and in the first days with the squabs (because of psychological aspects (which means motivation) and hormonal changes). Indeed we made the 8am and 2pm releases just before the expected hatchling, but the pair and group flights were done a few days earlier and thus, not during the peak time. Lipp [30] also showed in his study about nocturnal homing that breeding pigeons and pigeons with a high level of courtship activity appeared to be much better motivated for homing than other pigeons.

We decided to randomize the constellation of the duo and group flights but not the order (see above). Of course, further experiments with a randomized flight order would be interesting to verify our results, but we did consciously decide to use the non-randomized order. Bell [31] has recently written that a randomized order of treatments is often the best approach for an analysis. Yet she also pointed out that there are also several advantages for a fixed order, e.g. that all individuals have the same experience at each treatment. Precondition should be the assumption that, if there is a carryover effect, it should be similar for all individuals, or if individuals do differ in the carryover effect, then the variation among individuals in the carryover effect would be small relative to the mean amount of the carryover effect. If we assume that the carryover effect in our study is based on experience (or training, or learning), this precondition is met. To exclude a possible carryover effect of incubation time or incubation status and to ensure similar conditions for duos and groups, we made our 8am and 2pm releases just before the expected hatching but the duo and group flights a few days earlier and not during the peak time of incubation. Of course, monitoring and timing the breeding status in an experimental loft requires a lot of work and attention, which may explain at least part of the common neglecting this factor in studies.

The difficulty of reproducibility makes homing difficult to analyze in general. Aperiodic fluctuations have been found in the course of hours, from day to day, and among different years. And of course there is a high dependency on a) the actual weather and b) the release site, or more exactly the terrain between the release site and home, with its characteristic landmarks, geomagnetic field etc. [32]. But nonetheless, analyzing homing tracks can deliver exciting insights into birds' home finding processes. Our study give an insight in a special case (familiar route, short distance, nonstop flights) for which the efficiency index positively correlate with homing speed.

We would like to conclude by noting that our limited knowledge of pigeons' motivation to home is not only a problem of the evaluation and interpretation of homing data obtained with normal untreated birds. Even more so, this problem is relevant for investigations that use birds that are experimentally manipulated in a particular way. If their performance is reduced, it is necessary to ask whether the experimental interference reduced their ability or their willingness to home.

Supporting Information

S1 Table. Wind speed and wind direction for releasing times.
(DOCX)

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Formal analysis: JM.

Funding acquisition: GR.

Investigation: JM.

Methodology: JM.

Project administration: JM.

Resources: GR.

Software: JM.

Supervision: GR.

Validation: GR.

Visualization: JM.

Writing – original draft: JM.

Writing – review & editing: JM GR.

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