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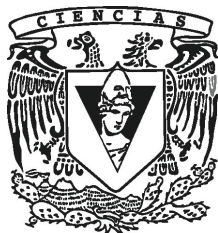
PERCEPCIÓN DE LA ILUSIÓN DELBOEUF POR EL GATO  
DOMÉSTICO ADULTO (*Felis silvestris catus*)

T E S I S

QUE PARA OBTENER EL TÍTULO DE:  
BIÓLOGA

P R E S E N T A:

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“Amar a las personas  
como se quiere a un gato:  
sin intentar domarlo,  
sin intentar cambiarlo,  
sin pedir nada,  
siendo feliz  
con su felicidad.”

*Como se quiere a un gato – Javier Salvago Calderón*

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## RESUMEN

### Introducción

En las últimas décadas, el estudio comparativo de la percepción de ilusiones visuales ha sido altamente reconocido como una herramienta no invasiva para comprender mejor la percepción visual, los mecanismos neuronales subyacentes y su evolución comparada entre distintas especies de vertebrados (Kelley & Kelley, 2014). La percepción visual de un objeto (por ejemplo: color, forma o tamaño) puede ser distorsionada por el ambiente circundante, provocando una ilusión visual (Gregory, 1997). Existen diferencias notables respecto a cómo se captura y procesa esta información visual en distintas especies. Entre vertebrados, incluso entre mamíferos, hay diferencias anatómicas en la estructura y posición de los ojos (Heesy, 2008; Veilleux & Kirk, 2014) y en sus circuitos neuronales subyacentes (Eagleman, 2001; Mascalzoni & Regolin, 2011), ambos moldeados por procesos evolutivos.

Estudios comparativos han revelado tanto similitudes como diferencias entre especies en la susceptibilidad a las ilusiones visuales geométricas, en cuanto al tamaño y figura de los objetos. Por ejemplo, la ilusión de Delboeuf es un tipo de ilusión visual que provoca una percepción errónea del tamaño de un objeto en función de su contexto circundante; fue descrita por primera vez en 1865 por el psicofisiólogo belga Joseph Delboeuf (Delboeuf, 1865). Estudios que se realizaron presentando esta ilusión a primates no-humanos encontraron que chimpancés, macacos, y monos capuchinos son susceptibles a la ilusión (Parrish & Beran, 2014, Parrish et al., 2015), mientras que en estudios realizados con perros se encontró que éstos no son capaces de percibirla (Petrazzini et al., 2016; Byosiére et al., 2017b).

Consideramos al gato doméstico (*Felis silvestris catus*) como una buena especie modelo para el estudio comparativo de susceptibilidad a una ilusión visual debido a que posee un sistema visual similar al de los primates, incluyendo humanos. Adicionalmente, una gran parte de la información neurofisiológica asociada al sistema visual que se tiene registrada proviene principalmente de estudiar al gato. Algunas de las razones por las cuales este mamífero ha sido el mayor sujeto en estudios electrofisiológicos son, por ejemplo, 1) tienen un gran sentido de la visión y 2) son fáciles y baratos de mantener, a comparación de otros animales de estudio como

los primates no humanos. Además, es difícil extrapolar información de un animal a otro, por lo que es importante investigar cómo los gatos realmente “ven el mundo” y cómo esto se manifiesta en su comportamiento antes de hacer una presunción seria de su información neurofisiológica (Mitchel, 1971).

Investigadores argumentan que hubo al menos dos episodios importantes de selección en el linaje que dieron lugar al gato doméstico: el primero ha sido asociado a la rápida declinación del tamaño corporal, el cual ocurrió al final del Pleistoceno y mucho antes de que la domesticación sucediera. El segundo episodio ha sido asociado con la domesticación misma, proceso que condujo a cambios en el cerebro, comportamiento y reproducción de la especie, aunque los efectos de la domesticación en la estructura del cerebro no han sido del todo profundamente estudiados (Williams et al., 1993). Además, Williams y colaboradores (1993) reportaron que existe una diferencia en el tamaño promedio del cuerpo entre la subespecie de gato salvaje español (el cual es morfológicamente más cercano al de la población del Pleistoceno), y el gato doméstico; lo anterior se puede observar claramente en la reducción de masa cerebral del linaje doméstico. En específico, las poblaciones de células ganglionares de la retina y las neuronas del núcleo genicular lateral (NGL) están reducidas un 30-35%, reducción que también encaja con la reducción total del peso cerebral, implicando que una rápida modulación evolutiva en el tamaño del cerebro fue generada principalmente por cambios en el número de células. Los investigadores también mencionan que este decrecimiento en el tamaño del cerebro en el linaje doméstico está probablemente asociado con un incremento en la incidencia de muerte celular, donde el mismo número de neuronas es generado tanto en el gato doméstico como en el gato salvaje, pero muchas de estas células son eliminadas subsecuentemente. Por lo tanto, las tasas de modulación de muerte celular -más que las tasas de producción celular- podrían ser una ventaja adaptativa en hacer posible rápidos cambios evolutivos en el tamaño de poblaciones neuronales interconectadas y por consiguiente, afectar el sistema visual del gato doméstico como especie.

Aunque el ojo del gato (y en general de los felinos) sigue el patrón de un mamífero regular, existen especializaciones que le permite ver el mundo de manera diferente a nosotros. Generalmente, comparado con el ojo humano, el ojo del gato está mejor adaptado a ver a muy bajas intensidades de luz; esto es debido a que tiene casi tres veces más bastones que nosotros,



combinados con la capa reflectora (*tapetum lucidum*) detrás de la retina (Bradshaw et al., 2012 en Turner & Bateson, 2014). No obstante, esta adaptación a la caza crepuscular también tiene sus costos, dejando menos espacio en la retina para los conos, los cuales detectan colores. Por lo tanto, los colores parecen tener un papel poco importante en cómo los gatos perciben e interpretan su ambiente (Turner & Bateson, 2014). Aunque el gato es considerado como un animal crepuscular, tiene una alta afinidad para sincronizarse con los humanos y volverse de hábitos más diurnos (Randall et al., 1985; Piccione et al., 2013). Algunos estudios han demostrado ritmos circadianos en su alimentación y patrones de actividad locomotora, y que son sensibles a los cambios de periodos de luz (Delmar Cerutti et al., 2018; Parker et al., 2019).

La investigación conductual empírica ha mostrado que los gatos pueden distinguir entre diferentes tamaños, formas y texturas de los objetos. Se ha comprobado que el gato doméstico percibe las ilusiones visuales de contornos subjetivos (Bravo et al., 1988; De Weerd et al., 1990), y la ilusión de la “serpiente rotatoria” (Bååth et al., 2014); y hay resultados preliminares de que pueden percibir la ilusión de Zöllner y la de Müller-Lyer. Los gatos también son capaces de discriminar cantidades (Pisa & Agrillo, 2009), incluso sin entrenamiento previo ya que pueden diferenciar entre cantidades diferentes de comida si la proporción es menor a 0.5 (Bánszegi et al., 2016). Adicionalmente, comparten un estilo de vida semiarbóreo (es decir, que regularmente se mueve y caza en tres dimensiones) similar al de la mayoría de los primates donde las medidas precisas de profundidad y distancia son vitales.

Por otra parte, en un número cada vez mayor de países, el gato es hoy uno de los animales de compañía más populares, por lo que hay gran interés en sus habilidades cognitivas. También por ello el gato se encuentra ampliamente disponible para experimentos simples (como el presente) a través de redes de dueños voluntarios. Es necesario enfatizar la importancia del estudio comparativo entre distintas especies usando métodos que permitan evaluar las presiones evolutivas y/o factores ambientales que hayan afectado a la susceptibilidad por parte de cada especie a las ilusiones visuales y que al mismo tiempo mantengan suficiente similitud como para poder asumir que involucran estructuras y procesos similares. También resulta importante que dichos métodos sean biológicamente relevantes para entender mejor la relevancia de las ilusiones visuales en un contexto lo mas cercano a el contexto natural.

## **Objetivo general**

Investigar si el gato doméstico adulto es susceptible a la ilusión de Delboeuf de manera similar a otras especies de mamíferos estudiadas hasta la fecha; ya sea si perciben la ilusión como los primates, con quienes comparten un estilo de vida semiarbóreo, o si no son susceptibles a ella como el perro doméstico, con quien está más cercanamente relacionado taxonómicamente.

## **Hipótesis de investigación**

Esperamos que en las condiciones control (donde dos diferentes cantidades de comida son presentadas en platos del mismo tamaño), los gatos elijan espontáneamente la cantidad grande de comida, como lo han realizado en previos experimentos similares (Bánszegi et al 2016).

Para la condición de la ilusión (donde la misma cantidad de alimento es presentada en platos de distintos tamaños), esperamos que los gatos elijan predominantemente el plato pequeño que simulará tener la mayor cantidad de alimento.

## **Método**

Para lograr que el desempeño de los gatos fuera comparable con las especies previamente estudiadas, seguimos la metodología utilizada para probar perros (Petrazzini et al., 2016) y primates (Parrish & Beran, 2014; Santacà et al., 2017), pero ligeramente modificada para hacer que la situación de estudio fuera más apropiada para nuestra especie: el gato doméstico.

### *Animales y tamaño de muestra*

En un principio se colectaron los datos de 25 gatos adultos (de 1 a 7 años de edad; de raza mixta) dentro del Área Metropolitana, pero se tuvieron que excluir cuatro gatos debido a que mostraban una fuerte tendencia a desviarse a un solo lado (p.ej. siempre elegían el plato que se encontraba en el lado derecho) durante las pruebas por tres sesiones consecutivas y otros tres individuos más debido a que no se encontraban motivados a realizar las pruebas por tres sesiones consecutivas.

Se reclutaron dueños voluntarios mediante un anuncio por internet para los estudiantes de la Facultad de Ciencias de la Universidad Nacional Autónoma de México. Los criterios de selección de los gatos fueron: (1) el gato debía tener al menos un año de edad; (2) debía ser amigable con desconocidos y no escapar o comportarse agresivo con los experimentadores; (3) el dueño debió aceptar que el gato ayunara de 4 a 6 horas antes de cada sesión (esto para motivarlos a hacer las pruebas) y (4) estar de acuerdo con que los experimentadores realizaran al menos ocho visitas a sus casas para hacer las pruebas (Byosiere et al., 2017b; Parrish & Beran, 2014; Parrish et al., 2015; Patrazzini et al., 2016; Santacà et al., 2017).

#### *Lineamientos bioéticos*

Todos los gatos del presente estudio son mascotas de compañía; las pruebas experimentales se llevaron a cabo dentro de sus hogares, en la presencia de sus dueños y bajo su previo consentimiento. El protocolo experimental siguió los lineamientos para el cuidado y uso de animales para investigación de la Asociación Psicológica Americana y la Norma Oficial Mexicana NOM-062-ZOO-1999, la cual especifica técnicas para la producción, cuidado y uso de los animales de laboratorio. Además, la metodología fue aprobada por el Comité de Ética y Responsabilidad Científica de la Facultad de Ciencias, Universidad Nacional Autónoma de México bajo el número de folio T\_2019\_02\_003.

#### *Alimento estímulo*

Debido a que los gatos muestran diferencias individuales marcadas en preferencias de alimento (Bradshaw et al., 1996; Bradshaw et al., 2000; observaciones propias), el experimentador identificó la comida preferida de cada individuo para así motivarlo efectivamente a esperar el estímulo y desempeñar cada una de las pruebas. Para ello, antes de comenzar el estudio, el experimentador brevemente ofreció a cada sujeto una prueba de tres diferentes alimentos: comida enlatada para gato, atún enlatado y croquetas para gato. El primer alimento que comiera el gato era el que se utilizaba para todos los ensayos de ese mismo individuo. Dos gatos fueron estudiados con croquetas para gato, 14 fueron probados con atún y otros dos fueron probados con comida enlatada para gato. Una investigación previa que se realizó en chimpancés (*Pan*

*trogloodytes*) para estudiar la ilusión de Delboeuf, encontró que el comportamiento de elección por el animal fue altamente consistente a través de diferentes tipos de alimento y que no causaba efecto en el desempeño si el alimento era “discreto” (p.ej. piezas de cereal) o “continuo” (p.ej. carne) (Parrish & Beran, 2014).

### *Condiciones y procedimiento experimental*

Cada gato participó en tres diferentes condiciones de elección espontánea de alimento: dos controles (diseñados para ver si el gato lograba diferenciar entre dos porciones distintas de alimento presentadas simultáneamente en platos de igual tamaño) y una tercera condición experimental donde se le presentó la ilusión de Delboeuf (la misma cantidad de alimento presentada simultáneamente en dos platos de distinto tamaño). En cada condición el alimento fue presentado en dos platos de plástico, los tamaños utilizados fueron: platos grandes de 12.5 cm de diámetro y platos pequeños de 9.5 cm de diámetro. Los platos se colocaban sobre un pliego de plástico de color gris (47 cm x 68 cm). Todas las pruebas se grabaron con una cámara de video (GoPro 4 Session, GoPro Inc., CA. USA) para su posterior análisis. Los animales no fueron trasladados a un laboratorio, sino que registramos las pruebas en sus respectivos hogares en un cuarto que fuera familiar para ellos, preferiblemente sin la presencia de sus dueños. Es importante mencionar que ninguno de los gatos recibió entrenamiento previo para llevar a cabo las pruebas experimentales.

Para realizar las pruebas se requerían dos experimentadores: Uno de los experimentadores colocaba los platos en cada una de las condiciones; luego, se alejaba y se ponía de espaldas a la prueba. Después, el segundo experimentador colocaba al sujeto de estudio sobre una silla para que tuviera una mejor vista de las dos cantidades de alimento y mientras miraba hacia al frente lo sujetaba gentilmente por 5 segundos para después soltarlo. El gato elegía espontáneamente una de las cantidades de alimento e inmediatamente podía consumirla.

Cada gato realizó en total 16 pruebas por cada condición (los dos controles y la condición experimental), pero participaban en 6 pruebas (dos por cada condición) en un solo día, por lo que nos llevó 8 días (o sesiones) realizar todas las pruebas, sumando al final un total de cuarenta y ocho pruebas por gato. La posición y orientación de los platos fue balanceada entre ensayos y el

orden de las condiciones fue aleatorio. Asimismo, se les dió a elegir a los gatos entre tres distintos tipos de alimento que se utilizaron en las pruebas: atún enlatado, croquetas para gato y comida enlatada para gato, esto lo decidimos para asegurar que se encontraran motivados a participar.

Tomamos en cuenta las variables individuales de cada gato como lo son: edad, sexo, estado reproductivo (esterilizado o no), alimento elegido (croquetas, atún o comida enlatada) y estilo de vida (exclusivamente interior, o interior y exterior a la vez) para posteriormente comparar su desempeño individual con respecto a los demás gatos e incluirlo en nuestro análisis estadístico.

### *Análisis estadístico*

Se realizó con el programa R (R Core Team, 2017), versión 3.4.1. El desempeño individual se analizó mediante una prueba binomial mientras que los valores a nivel poblacional fueron analizados con estadística paramétrica (prueba de Shapiro-Wilk). Para determinar si los gatos discriminaron entre las cantidades de alimento (pruebas control) y si percibieron la ilusión se usó la prueba t de Student para una muestra. Además, para analizar y comparar el desempeño de cada gato con sus respectivas variables, se usó la prueba de t de Welch para muestras no iguales. Finalmente, se calculó la d de Cohen para estimar el tamaño de los efectos.

## **Resultados**

### *Condiciones control*

Los individuos eligieron la cantidad grande de alimento más veces en ambas condiciones control (plato grande y plato chico). El desempeño del grupo fue significativo, aunque a nivel individual solamente dos de los 18 gatos tuvieron un desempeño significativo, (dos en control “plato grande” y dos en el control “plato chico”). Adicionalmente, se encontró una correlación positiva significativa entre el desempeño de los gatos en las dos condiciones de control ( $p < .05$ ), y no hubo ninguna diferencia en el desempeño del grupo en las dos condiciones ( $p = .10$ ).

No se encontró ninguna correlación entre el porcentaje total de los gatos que eligieron la cantidad grande de comida para cualquiera de las condiciones de control y el orden de las pruebas, sugiriendo que no hubo efectos de aprendizaje significativos en las pruebas control durante el

estudio. Tampoco se encontraron diferencias significativas en el desempeño debidas al sexo, edad o estado reproductivo. Sin embargo, se encontró una diferencia significativa asociada al estilo de vida. En general, los gatos que habitan en interior y exterior eligieron la porción de alimento grande más frecuentemente que los gatos que son exclusivamente de interior.

#### *Condición experimental (ilusión de Delboeuf)*

En las pruebas de la ilusión de Delboeuf, los 18 gatos eligieron significativamente más veces la comida que fue presentada en el plato chico que en el grande, lo que sugiere que fueron susceptibles a la ilusión de Delboeuf. Sin embargo, a nivel individual ninguno de ellos desempeñó significativamente. Tampoco se encontraron diferencias significativas en el desempeño debidas al sexo, edad o estado reproductivo. Asimismo, no se encontraron correlaciones entre la edad y el desempeño, entre el desempeño general en las pruebas de control y el desempeño en la ilusión, ni entre el desempeño de los gatos en las pruebas de condición experimental y el orden de las pruebas, sugiriendo que no hubo efectos de aprendizaje entre las pruebas de la ilusión.

#### **Discusión**

Los resultados de las dos condiciones control confirman que los gatos no necesitaron de entrenamiento previo para poder distinguir entre las diferentes cantidades de alimento presentadas puesto que eligieron significativamente más veces la cantidad grande, al menos a nivel de grupo. A pesar de este hallazgo, a nivel individual solamente dos individuos eligieron la cantidad grande de alimento en más ocasiones de lo esperado por azar en la condición de control con el plato grande; lo mismo para cuatro individuos en la condición control con el plato chico. Sin embargo, cuando combinamos los datos de las dos condiciones de control (ya que el desempeño grupal no difirió entre estos dos), el 50% de los gatos mostró una preferencia significativa por la cantidad grande de comida a nivel individual.

En el caso de la condición experimental, la ilusión de Delboeuf, obtuvimos la primera evidencia que sugiere que los gatos, así como los humanos (McClain et al., 2014; Van Ittersum & Wansink, 2012) y algunos primates no humanos (Parrish & Beran, 2014; Parrish et al., 2015), son

también susceptibles a esta ilusión. Este resultado puede ser explicado por el hecho de que todos los gatos eligieron el plato pequeño más veces. Además, esto fue cierto incluso cuando la posición de los estímulos (alimento) y la colocación del diseño experimental dentro del hogar de los dueños fue aleatorio en todas las pruebas. De manera consistente con previos hallazgos en la discriminación de cantidad de alimento por coyotes (Baker et al., 2011), perros (Ward & Smuts, 2007), gatos (Bánszegi et al., 2016) y ratas (Wadhera et al., 2017), los individuos del presente estudio debieron haber elegido cualquiera de los dos estímulos presentados por prueba solamente a partir de señales visuales. Las señales olfativas no podrían haber formado parte a la hora de tomar su decisión ya que las porciones de comida en la condición experimental fueron del mismo tamaño.

Relativamente hablando, existe poca literatura sobre la percepción de ilusiones visuales (incluyendo la ilusión de Delboeuf) para comparar entre especies de mamíferos. Es por ello que intentamos hacer nuestros métodos comparables con al menos algunos de los estudios previos hechos con primates (Parrish & Beran, 2014; Santacà et al., 2017) y con el perro doméstico (Petrazzini et al., 2016). Mientras que nuestros resultados indican que los gatos (al igual que varios primates no humanos) son susceptibles a la ilusión, éstos contrastan con los reportes donde mencionan que el perro doméstico no es capaz de percibirla. Algo interesante que se encontró fue que algunos perros fueron susceptibles a la ilusión pero en dirección contraria a la de los humanos, otros primates y los gatos de este estudio (Byosiére et al., 2017b; Petrazzini et al., 2016). Una posible explicación para estas diferencias entre perros y gatos podría ser las diferencias que existen en la metodología experimental. A diferencia de los estudios con canes arriba mencionados, nosotros decidimos realizar las pruebas con los gatos en sus casas y con su alimento preferido para así reducir el nivel de estrés e incrementar la motivación para desempeñar las pruebas. Aunado a esto, fueron evaluados inicialmente desde una posición elevada, y no a nivel de piso, para así darles una visión clara y no distorsionada de los dos estímulos. Pero quizás más importante, aún no es muy claro si la proporción efectiva de la diferencia de tamaño entre el estímulo (ej. alimento) y su contexto circundante (ej. tamaño del plato) sobre la cual depende la ilusión de Delboeuf difiere entre especies. En el presente estudio, siguiendo a Petrazzini et al. (2016) para propósitos comparativos, durante las pruebas de ilusión los gatos discriminaron entre

proporciones alimento-plato de 0.5 (en el plato chico) y 0.36 (en el plato grande), prefiriendo elegir el estímulo con la proporción de 0.5, donde la orilla del plato bordeaba el alimento más cerca.

Aún no existe una explicación convincente sobre por qué algunas especies son susceptibles a la ilusión de Delboeuf y otras no aún, pero el análisis de las diferencias en el diseño experimental y métodos de cómo se llevaron a cabo estos estudios podrían contribuir potencialmente a esclarecer dicha situación. Por ejemplo, estudios difieren entre el uso de pruebas de elección espontánea o, de un entrenamiento extensivo. Mientras que las pruebas de elección espontánea muestran cómo los animales se comportan en situaciones más apegadas a la naturaleza, estudios usando individuos previamente entrenados son más útiles para explorar las habilidades perceptuales o cognitivas de las especies (Agrillo & Bisazza, 2014). Otra inconsistencia metodológica es si los sujetos son probados con estímulos alimenticios o no ecológicos (ej. pantallas táctiles), y si son premiados en caso de haber elegido una opción en particular, pues ambos factores pueden influenciar en la motivación de los animales. En este estudio, pusimos a prueba la elección espontánea de los gatos con el objetivo de explorar sus tendencias perceptuales naturales.

Un hallazgo notable del presente estudio fue la falta de correlación entre el desempeño individual en las condiciones de control y el desempeño en la condición experimental. Es decir, los individuos que fueron más precisos en elegir el alimento grande en las pruebas de control no necesariamente mostraron una susceptibilidad mayor a elegir el estímulo de la ilusión de Delboeuf durante la condición experimental, a pesar de que los gatos fueron susceptibles a nivel de grupo. Una posibilidad es que, mientras un individuo discrimine el tamaño de un objeto sin un contexto que lo distorsione, dependa principalmente de mecanismos de la periferia conocidos como bottom-up, (que quiere decir que la cadena de eventos comienza con el estímulo externo, antes de progresar hacia arriba a través de las varias etapas de procesamiento mental y culminando finalmente en la experiencia visual (McLeod, 2018)) y que la percepción de ilusiones es el producto de un proceso más central del cerebro conocido como top-down, donde la información sobre lo que estamos mirando viaja desde altas regiones corticales cuesta abajo hacia el córtex visual, generando una experiencia visual que es creada internamente en el cerebro y que no es un reflejo del mundo real (Gilbert & Li, 2013), y que posiblemente dependa de procesos tempranos de



maduración y/o experiencia ganada durante el desarrollo. La utilidad de la cognición “top-down” es que permite que el cerebro llene los espacios de nuestro campo visual trayendo previas experiencias y entendimiento de cómo nuestro mundo debería de ser, generando una imagen visual que esperaríamos ver. Generalmente, estos dos procesos se complementan mutuamente a la perfección, aunque las ilusiones ópticas demuestran lo fácil que es engañar al cerebro en algo tan simple porque éste ya había esperado ver algo en concreto incluso cuando en realidad no está allí, creando “bucles de retroalimentación” que complementan el estímulo externo ya visto por los ojos (Pafundo et al., 2016).

Respaldando esta posible explicación, se ha reportado que los niños menores a los 7 años de edad son capaces de discernir entre el tamaño de un objeto-diana con gran precisión, pero no es sino hasta después en su desarrollo que se vuelven susceptibles a la influencia de contextos engañosos, creando así ilusiones visuales (Doherty et al., 2010; Káldy & Kovács, 2003; Parrish et al., 2016). Ya que los circuitos neuronales que median la capacidad de percibir ilusiones probablemente involucren áreas corticales más elevadas (Livingstone & Hubel, 1988), la conectividad que apoya la sensibilidad contextual puede no estar completamente desarrollada a una edad tan temprana (Káldy & Kovács, 2003). Esto es congruente con la investigación realizada por Poirel y colaboradores (2011), donde explican que la pérdida de materia gris en las áreas derecha parietal y visual de los niños de aproximadamente 6 años de edad, pueda verse reflejada en la madurez anatómica.

Además, en estudios transculturales Fujita y colaboradores (2017) encontraron diferencias en la susceptibilidad a diferentes ilusiones entre la gente de distintas culturas, lo que sugiere una importante contribución de la experiencia o también conocido como “factor de aprendizaje” a la percepción ilusoria. En estudios del desarrollo se ha visto que distintas ilusiones visuales siguen diferentes cursos en el desarrollo. No obstante, los resultados no son siempre convergentes, probablemente debido a los diferentes y únicos caminos de desarrollo que las ilusiones pueden seguir para ser asimiladas. Es claro que las ilusiones visuales no son exclusivas para la visión humana, lo que nos sugiere un contexto evolutivo donde este fenómeno perceptivo fue aparentemente favorecido por la región del cerebro que se encarga de analizar los estímulos ambientales. Es así que Fujita y colaboradores (2017) también sugieren que las ilusiones visuales

son una consecuencia de estos ajustes o limitaciones adaptativas involucradas en la función de procesamiento del sistema visual en situaciones inapropiadas (o engañosas) para el cerebro.

Se necesitará de más investigación donde los gatos sean probados con diferentes tipos de ilusiones visuales, lo cual podría ayudar a revelar diferencias en el procesamiento de información visual incluso comparada, por ejemplo, con otros carnívoros. Adicionalmente, tomando en cuenta al gato doméstico como un modelo experimental accesible, surgen las preguntas de cuándo durante el desarrollo las crías se vuelven capaces de discriminar, por ejemplo, diferentes cantidades de alimento, y a qué edad se vuelven susceptibles a la ilusión de Delboeuf.

## ABSTRACT

The comparative study of the perception of visual illusions between different species is increasingly recognized as a useful non-invasive tool to better understand visual perception, its underlying mechanisms and evolution. The way many animal species obtain a significant amount of the information about their environment is via their visual systems, which can be captured and processed differently across species. A visual illusion is when the visual assessment of a target object can be distorted by the surrounding environment. One of the most common geometrical illusion examples is the Delboeuf illusion, which is formed by a single ring surrounding the target stimulus, causing the target stimulus to be perceived as larger or smaller depending on how closely the inducer ring border it.

The domestic cat (*Felis silvestris catus*) is considered a good candidate species for such comparative study due to its high dependence on visual cues, their three-dimensional movements in order to hunt (similarly to most primates) and being able to perceive subjective contours and a motion illusion. The aim of this study was to test whether the domestic cat is susceptible to the Delboeuf illusion in a manner similar to other mammalian species studied to date. For comparative reasons, we followed the methods used to test domestic dogs and different primate species. In two different types of control trials, 18 cats discriminated between two different amounts of food presented on same-size plates and they spontaneously chose the larger amount, as has been previously reported for other species, suggesting that the method used here was adequate to test cats. In the Delboeuf illusion trials, two equal amounts of food were presented on different-size plates; all tested cats chose the food presented on the smaller plate more often than on the larger one, suggesting that they were susceptible to the illusion. Since we found no correlation between the cat's overall performance in the control trials and their performance in the illusion trials, we propose that the mechanisms underlying spontaneous size discrimination and illusion perception might be different.

## INTRODUCTION

### *Visual system related to visual illusions*

The visual system is the part of the nervous system which allows organisms to see and to interpret the information from their environment in order to build a representation of the world surrounding them. However, visual signals are often ambiguous because a 3D form or scene must be translated into a 2D retinal representation that is subsequently interpreted by neurological and cognitive processes occurring in the brain to generate a perceptual experience (Coren and Girgus, 1978; Feng et al., 2016).

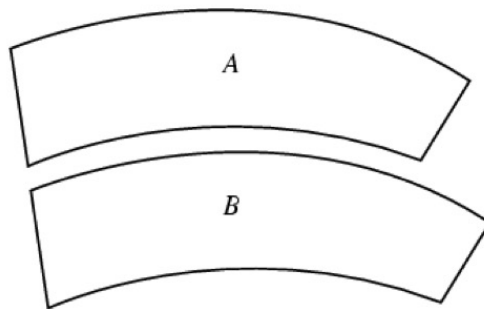
Many animal species obtain a significant amount of the information about their environment via their visual systems. However, the way this sensory information is captured and processed can vary notably across species. Within vertebrates and even within mammals these differences originate from anatomical differences in the structure and position of the eyes (Heesy, 2008; Lamb, Collin, & Pugh, 2007; Veilleux & Kirk, 2014) as well as their underlying neural circuits (Eagleman, 2001; Mascalzoni & Regolin, 2011; Masland & Martin, 2007), both shaped by evolutionary processes. However, the visual assessment of a target object, e.g. its colour, shape or size, can be distorted by the surrounding environment, leading to so-called visual illusions (Gregory, 1997).

### *Visual illusions*

Humans have long been known to perceive a wide range of optical illusions (Wade, 2017), and the comparative study of illusions between humans and non-human mammals is increasingly recognized as a non-invasive tool to better understand visual perception, its underlying mechanisms and evolution.

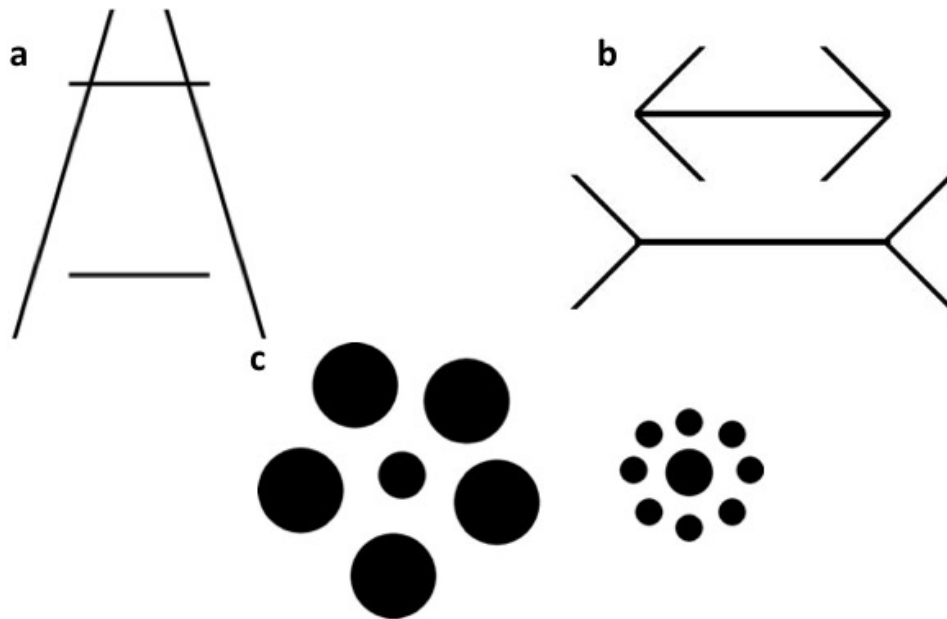
Studies investigating non-human animals' perception of geometrical illusions date back to the 1920's. Révész (1924) tested a hen with the Jastrow illusion (figure 1) and he found that the bird, which was previously trained to choose the smaller size between two different-sized figures chose more times the subjectively smaller segment of the figure that represented the illusion rather than choosing the apparently larger one. Révész was an

exception with his experiment and findings since during the next decades animals were still considered as machines perceiving exact replicas of the inputs they receive; therefore, scientists were not interested in perception and optical illusion in animals. Apart from a few exceptions it was until the 21st century when this view began to change and researchers started to realize that animals probably are more similar to humans in this sense, they alter visual inputs too and moreover, some species even actively manipulate their environment to create visual illusions (Feng et al., 2016).



**Figure 1.** Diagram of the **Jastrow illusion**. It consists in two equal-size segments which are placed one above the other; the upper segment (A) will be perceived smaller in comparison to the lower one (B) although their size is the same (Révész, 1924).

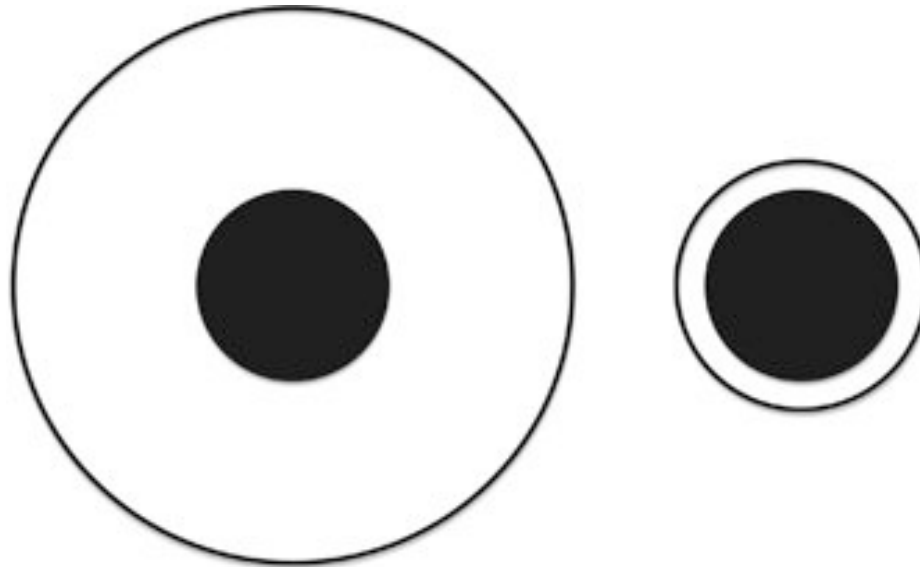
Comparative studies have revealed both similarities and differences in susceptibility to geometrical visual illusions (pertaining to an object's size and shape) across species. It seems that in general most mammals are susceptible to at least some geometrical optical illusions (e.g. 11 of 12 tested vertebrate species have been found to be susceptible to the Ponzo (figure 2A) and Müller-Lyer (figure 2B) illusions in the same manner as humans), albeit with some notable differences. The Ebbinghaus illusion (figure 2C) which has been amply studied in a variety of species with different ecological and taxonomical backgrounds, not yet no discernible pattern is apparent in their susceptibility to the illusion nor the direction in which it is perceived. Whereas some species reportedly lack susceptibility to certain illusions others have been found to be susceptible in the opposite direction to humans (see reviews in Feng et al., 2017; Kelley & Kelley, 2014).



**Figure 2. Diagrams of some of the most common geometrical illusions. A. Ponzio illusion:** two lines of equal length that are framed by a set of converging lines, making the upper line seem longer than the one in the bottom. **B. Müller-Lyer illusion:** two lines of same length are presented; one has outward-pointing arrows on the ends while the other line has inward-pointing arrows on the ends. Some animals (including humans) perceive the inward-pointing arrows' line longer than the line with the outward-pointing arrows. **C. Ebbinghaus illusion:** two equally sized circles are presented; one is surrounded by small circles while the other is surrounded by large circles. For some mammals (including humans), the target circle surrounded by the small circles seems larger than the other one (Kelley & Kelley, 2014; Feng 2017).

### *Delboeuf illusion*

One of the most common geometrical illusions is when the size of a target object is misperceived because of its immediate surround. If the size of the target stimulus is processed globally (taking into account its surround) rather than locally (taking into account only its own physical dimensions), then the actual size of the target may be misperceived (Navon, 1977). A classic example is the Delboeuf illusion (Delboeuf, 1865), which is formed by a single ring surrounding the target stimulus, causing the target stimulus to be perceived larger or smaller depending on how closely the inducer ring borders it (Figure 3). In humans, typically out of two target objects of the same size the one bordered more closely by an inducer ring is perceived as larger (Mruczek, Blair, Strother, & Caplovitz, 2017). One theoretical explanation for the perception of the Delboeuf illusion is the assimilation-contrast theory: if the target stimulus and its inducer ring are close together, they will merge and be perceived as one, whereas if the inducer circle is farther away from the target object (it does not circle it closely), this creates a distinction between the two, hence the target object appears to be smaller (Girgus, Coren, & Agdern, 1972; Goto et al., 2007; Oyama, 1960). The contour interaction theory is another, not necessarily competing theory, which proposes that the contours that are proximal to an object perceptually attract while contours that are further away and exceed a certain distance perceptually repel, which in turn causes a change in apparent size (Jaeger, 1978). The Delboeuf illusion is even used commercially; for example, a food portion on a small plate appears larger than the same amount of food on a larger plate, thus influencing and exploiting human's misperception of a target object's size (Davis, Payne, & Bui, 2016; Murphy, Lusby, Bartges, & Kirk, 2012; Van Ittersum & Wansink, 2012; Wansink & Van Ittersum, 2013).



**Figure 3.** Diagram of the **Delboeuf illusion**. It's consists in two equally sized target circles where one is surrounded by a small ring and the other by a larger ring. Besides humans, some non-perceive the target circle surrounded by the smaller ring larger than the other one (Kelley & Kelley, 2014).

#### *Perception of the Delboeuf illusion by non-human mammals*

Susceptibility to the Delboeuf illusion has been reported in several non-human mammals, but because these studies have been conducted only in few species and the methodological differences between them are considerable (e.g. trained or spontaneous testing, whether the target object was food or stimuli presented on a touch screen; further details in the Discussion), not many comparative conclusions can yet be drawn. Generally it seems that non-human primates perceive the Delboeuf illusion in a manner akin to humans (chimpanzees *Pan troglodytes*, [Parrish & Beran, 2014]; rhesus monkeys *Macaca mulatta* and capuchin monkeys *Cebus apella*, [Parrish, Brosnan, & Beran, 2015]; but also see preliminary results on ring-tail lemurs, *Lemur catta* [Santacà, Regaiolli, Petrazzini, Spiezio, & Agrillo, 2017]. On the other hand, dogs (*Canis lupus familiaris*) do not appear to perceive the Delboeuf illusion, at least at the population level (Byosiere et al., 2017b; Petrazzini et al., 2016, but note that in the first study two dogs did appear to demonstrate susceptibility,



although in the opposite direction to humans). Consequently, there is a need for more cross-species comparisons using similar methods to be able to assess which evolutionary pressures and/or environmental factors affect a species' susceptibility to such illusions (Feng et al., 2017), and also to better understand their possible relevance in natural contexts (review in Kelley & Kelley, 2014 and see also Doerr & Endler, 2015; Griggio et al., 2016; Møller, 2017).

#### *The domestic cat (Felis silvestris catus)*

Psychologists have studied illusions in the hope that an understanding of the “errors” of perception might lead to understanding the mechanisms of perception (Mitchel, 1971), with the aim of this is to correlate specific brain activity with visual perception. However, nearly all the neurophysiological data associated with visual systems from animals other than man, is primarily from cats. Already a considerable amount of neurophysiological data gathered from the cat and there are several reasons why this mammal has been the major subjects in electrophysiological studies, e.g. they have good sense of vision, (2) easy and cheap to keep compared to primates. Since it is hard extrapolating data from one animal to another, therefore it is important to investigate how cats really “see the world” and how it’s manifest in their behaviour, before making any serious assumption from its neurophysiological data (Mitchel, 1971).

Another reasons why the domestic cat is a good model species are that it depends in large part on visual cues (like the previous species mentioned above) which are likely similar to those used by other mammalian species, including humans, to navigate in their environment (see for some comparision Blake, 1979; Byosiere et al., 2017a; Miller & Murphy, 1995). Like dogs, it belongs to the order Carnivora but in contrast, it has a semi-arboreal lifestyle more similar to primates. It regularly moves and hunts in three dimensions, similarly to most primates, where the precise assessment of depth and distance is vital. Finally, there is an increasing interest in cat’s cognitive abilities due to its popularity as one of the most common companion animals (American Pet Products Association, 2015; Gunn-Moore et al., 2007; Vitale Shreve & Udell, 2015, Bernstein, 2007; Driscoll et al., 2009).



**Figure 4.** The domestic cat (*Felis silvestris catus*)

#### *Domestic cat's visual system*

Researchers discuss that there have been at least two remarkable episodes of selection in the lineage that led to the domestic cat: the first one has been associated with a rapid decline in body size occurred at the end of the Pleistocene (and long before domestication happened). The second one has been associated with domestication, a process that led to changes in brain, behaviour and reproduction, although the effects of domestication on brain structure have not yet been deeply studied (Williams et al., 1993). They have also shown that the difference in average body size of the Spanish wildcat subspecies (which is morphologically closest to the Pleistocene stem population) and the domestic cat is enough to account for the observed reduction in brain mass in the domestic lineage. It has been shown that the populations of retinal ganglion cells and neurons in the lateral geniculate nucleus (LGN) of the domestic cat are reduced by 30-35%, which matches the reduction in total brain weight. Researchers also mention that this decrease in brain size in the domestic

lineage is probably associated with an increase in the incidence of cell death. The same numbers of neurons are generated in the domestic cat as in the wildcat, but that many more of these cells are subsequently eliminated. Thus, the modulation of rates of cell death rather than of rates of cell production could be of selective advantage in making possible rapid and well-matched evolutionary changes in the size of interconnected neuron populations and therefore, affecting the visual system of the domestic cat as species (Williams et al., 1993).

Neurophysiology of the vision of the cat is probably one of the best understood among non-primate mammals. Although the cat's eye follows to the regular mammalian pattern, there are specializations that allow it to see the world differently from us. Generally, compared to the human eye, the eye of the cat is better adapted to see at very low light intensities; this is because it has almost three times more rods than us, combined with the reflective layer (*tapetum lucidum*) behind the retina (Bradshaw et al., 2012 in Turner & Bateson, 2014). This adaptation to crepuscular hunting, however, has its costs too, allowing less space on the retina for the colour-detecting cones; their density of cones is six times lower compared to humans. Thus, it seems rather certain that cats can only see blue and green colours and their corresponding combinations, and not being able to see the colour red. Therefore, colours seem to play little importance in the way cats perceive and interpret their environment (Turner & Bateson, 2014).

The innervation of the eye is also organized in a different way; the regular human's optic nerve contains ten times more fibres than that of the cat, and there is an even greater variance in the density of ganglia in the retina. Overall, this leads to more rods and cones being connected to each nerve, causing greater sensitivity and therefore better night vision (Bradshaw et al., 2012). When the pupil is completely open, retinal illumination is of the same size as that of nocturnal creatures such as the badger and bat whereas diurnal primates, such as man and the chimpanzee, have about five times less retinal illumination (Bradshaw et al., 2012). Even though the cat is considered crepuscular it has a high affinity to synchronize with humans and become more diurnal (Randall et al., 1985; Piccione et al., 2013). Some studies have shown circadian rhythms in their feeding and locomotor activity patterns and that they are sensitive to changes in light periods (Delmar Cerutti et al., 2018; Parker et al., 2019).

Detection of movement is necessary for hunting, but it seems that cats are not good at detecting slow movements (Bradshaw et al., 2012). However, they are able to track and follow fast movements (e.g. a bird or other prey target) by performing very fast saccades while the object is being monitored the whole time and the sensory information is processed by the nervous system (Turner & Bateson, 2014). The ability of a cats to shift focus may also depend on their early visual experience: whereas outdoor cats tend to be rather long-sighted, indoor cats tend to become short-sighted; this is explained because the furthest objects on which they can focus are only a few meters away (Bradshaw et al., 2012). Cats seem slower to focus from close to distant objects and vice versa than humans and appear not to be able to focus objects closer than approximately 25 cm away or closer (Turner & Bateson, 2014). Their total visual field goes to approximately 200° and with binocular vision in the central 90-100°, while visual field of the human vision is approximately 180° (Traquair, 1938).

#### *Studies done with the domestic cat referring to visual illusions*

Despite the cats reduced colour perception, empirical behavioural research has shown that cats can distinguish differences in size, shape and texture of objects. In previous studies it has been shown that cats discriminate between quantities (Pisa & Agrillo, 2009), and do so even without training. Out of two different quantities of food, they spontaneously and reliably choose the larger one if the size ratio between them is below 0.5 (Bánszegi et al., 2016). They also perceive subjective contours (Bravo et al., 1988; De Weerd et al., 1990, Figure 5A and 5B) and a motion illusion (Bååth et al., 2014, Figure 5C). Mitchel (1971) also showed some preliminary results in her thesis that cats probably perceive the Zöllner illusion (Figure 5D) and the Müller-Lyer illusion (Figure 2B).

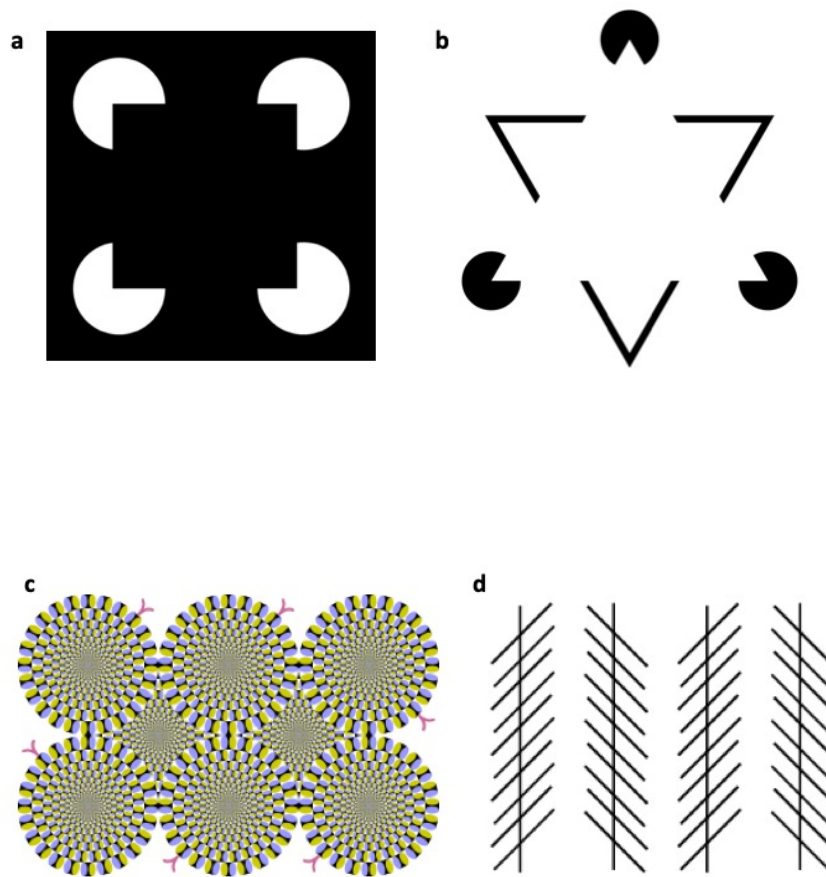


Figure 5. Diagrams of some visual illusions studied with the domestic cat. **A. Square subjective contour illusion:** Four white sectored circles generate a black illusory figure in the middle; in this case it forms an illusory square (Bravo et al., 1988). **B. Triangle subjective contour illusion:** The edges of these three black circles are coloured in white, generating a white illusory triangle in the middle. **C. Rotating snake motion illusion:** This is a type of illusion depends on the arrangement of the colours and their different luminance; in a certain order they are causing an illusory movement of the circles while in another arrangement they don't (Bååth et al., 2014). **D. Zöllner visual illusion:** This is a geometrical illusion where in two parallel lines are added small diagonal lines, causing that the parallel lines do not seem like that at all.

## AIM OF THE STUDY AND JUSTIFICATION

The aim of this study was to test whether the domestic cat is susceptible to the Delboeuf illusion, either in a manner similar to the primate species studied to date possibly due to the similarities in life-style (e.g. semi-arboreal, moving in 3-dimensions to a greater degree than other carnivores), or rather similar to the taxonomically more closely related domestic dog.

## RESEARCH HYPOTHESIS

In the control trials where two different quantity of food presented to the cats, we expect that they will spontaneously choose the larger amount as they reliable did in previously in similar experiments (Bánszegi et al 2016). If cats perceive the Delboeuf illusion under the same experimental conditions then we expect that during the illusion trials they would predominantly choose the one presented on the smaller plate from the two same size food stimuli, as this stimulus should appear to be larger.

## METHODS

In order to make the cats' performance comparable to previously tested species we followed the methods used to test dogs (Petrazzini et al., 2016) and primates (Parrish & Beran, 2014; Santacà et al., 2017), but adjusted slightly to make the test situation more species-appropriate for the cat.

### *Ethics Note*

Animals in this study were all household pets tested in their own homes in the presence of their owners, and with the owners' informed consent. The experimental protocol complied with the guidelines for the care and use of animals in research of the American Psychological Association, and with the National Guide for the Production, Care and Use of Laboratory Animals, Mexico (Norma Oficial Mexicana NOM-062-200-1999) and with approval by the

Ethics and Scientific Responsibility Committee (CERC, permission ID: T\_2019\_02\_003) of the Faculty of Sciences, Universidad Nacional Autónoma de México (UNAM).

### *Animals, Housing and Sample Sizes*

As in a previous study (Bánszegi et al., 2016), cat owners interested in participating in the study were recruited via an internet advertisement sent to students of the Faculty of Sciences, UNAM. The advertisement included a brief description of the study and listed the following inclusion criteria: (1) The cat should be at least one year old; (2) it should be friendly towards strangers, not fleeing from or behaving aggressively toward them; (3) agreement to deprive the cat of food for 4 h before each test session; and (4) agreement to have experimenters visit and test the cat on at least eight separate occasions. Most owners evaluated their cats appropriately, although we had to reject four cats prior to testing because they were not calm enough with strangers present to be easily handled during the experiments.

We began the tests with a total of 25 cross-breed cats but had to exclude four which exhibited a strong lateral bias (defined as the cat always going to the same side during the tests on three consecutive test days regardless of the stimuli presented), and three more cats that were not motivated to perform the tests on three consecutive test days. The remaining 18 cats finally included in the study were 10 males (four intact and six neutered) and eight females (three intact and five neutered), average age 2.9 years  $\pm$  0.4 SEM. Ten were exclusively indoor cats and the rest were indoor/outdoor cats (see Table 1 in Annex). None had received any training with the test procedures prior to the experiments.

### *Food Stimuli*

Since cats show marked individual differences in food preference (Bradshaw et al., 1996; Bradshaw et al., 2000; own observations), the experimenter identified a food preferred by each cat to effectively motivate it to attend to the stimuli and to perform the tasks. To this end, prior to the start of testing, the experimenter briefly offered each cat an array of three different foods: the cat's usual canned food, canned tuna and dry cat food. The first food

eaten by the cat was the stimulus used in all trials with that individual. Two cats were tested with canned cat food, 14 were tested with canned tuna and two were tested with dry food. A previous study of the presence of the Delboeuf illusion in chimpanzees (*Pan troglodytes*) found that animals' choice behaviour was highly consistent across different types of food, and it had no effect on performance whether the food was a "discrete" or a "continuous" type (cereal pieces or lunch meat, respectively; Parrish & Beran, 2014).

### *Experimental Setup*

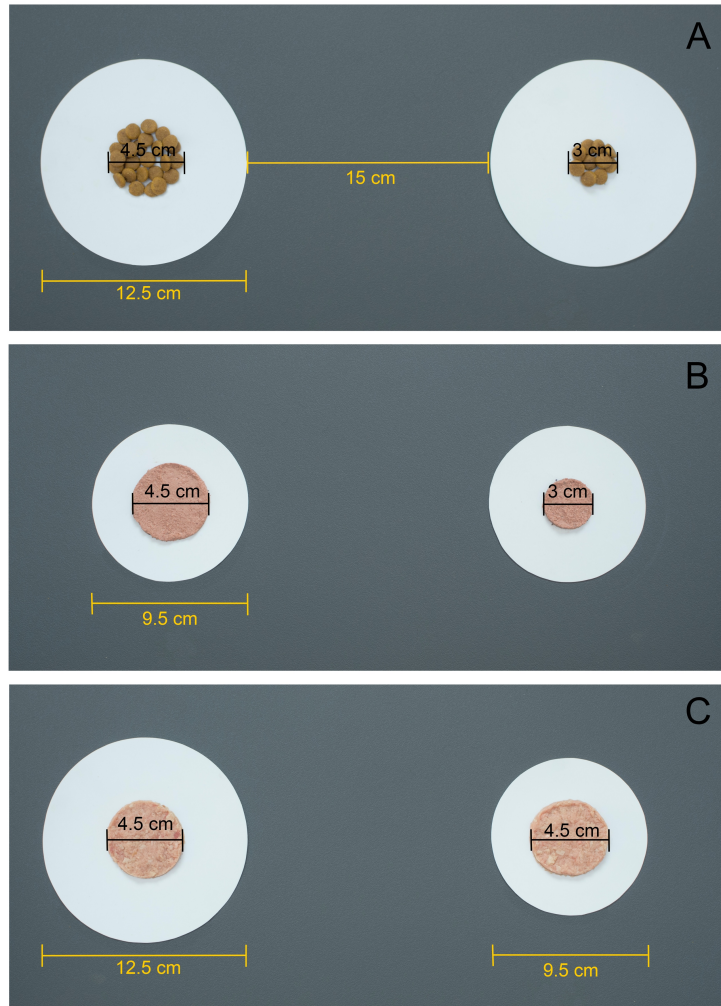
Each cat participated in three different spontaneous two-way food choice tasks. For comparative purposes we closely followed the methods previously used to test dogs (Petrzini et al., 2016) and primates (Parrish & Beran, 2014; Santacà et al., 2017), although adjusting them slightly for cats. These adjustments included (i) resizing the food and plates: we reduced the size of both since cats are smaller-sized mammals (see details below); (ii) the cats were able to go to and eat immediately from the chosen food like the dogs, but unlike the primates, which were only able to point to the preferred food quantity (see details below); (iii) all cats were tested in their home environment with a preferred food to keep them motivated (see above); (iv) we tested the cats only in one standard illusion trial and they received only 6 trials a day to maintain their motivation and avoid satiation (see details below); (v) finally, the starting point for the cats was not at floor level, instead they were placed at a certain height to give them a better visual angle (see details below).

The cats were tested individually in their home environment. The food stimuli were presented on white plastic plates of two different sizes: large plates 12.5 cm in diameter, and small plates 9.5 cm in diameter. In the center of each plate the food was formed into a circle using molds of two different sizes: a larger portion 4.5 cm in diameter and 0.2 cm high (volume = 3.18 cm<sup>3</sup>), and a smaller portion 3 cm in diameter and 0.2 cm high (volume = 1.41 cm<sup>3</sup>). The plates were presented on the floor on a washable matte grey plastic sheet (47 cm × 68 cm), 15 cm apart (distance between the edges of the plates). We used a chair as the starting point to provide the cat with a non-distorted overview of the nearly flat stimuli (chair



height: 48–50 cm, placed 25 cm from the edge of the plastic sheet). All tests were video recorded (GoPro 4 Session, GoPro Inc., CA. USA) for later analysis.

All cats were tested in three stimulus conditions: (1) Large plate control: two different food portions were presented on two large plates (Figure 6A); (2) Small plate control: two different food portions were presented on two small plates (Figure 6B); (3) Illusion: two equal, large food portions were presented on different-size plates (one large plate and one small plate; Figure 6C). The two types of control conditions were set up to test whether the cats would choose the larger portion of food in the two contexts (plate size). Based on previous studies mentioned in the introduction, we expected that in the control trials the cats would spontaneously choose the plate with the larger quantity of food. If cats perceive the Delboeuf illusion under these experimental conditions, then we expected that during the illusion trials they would predominantly choose the food stimulus presented on the smaller plate, as this stimulus should appear to be larger. In both control conditions, the ratio of the surface area between the smaller and the larger food portions was equal to .44, which was found sufficiently distinct for cats to perceive in a previous study of spontaneous quantity discrimination, as below ratios of 0.5 the cats chose the larger of two amounts of food significantly above chance (Bánszegi et al., 2016).



**Figure 6.** The three stimulus conditions which were presented in random order multiple times to each cat. A) **Large plate control** in which different quantities of the same food, in this example dry cat food, were presented on large, same-size white plastic plates, with food-to-plate diameter ratios: .36 (large food) and .24 (small food). B) **Small plate control** in which different quantities of the same food, in this example canned cat food, were presented on small, same-size white plastic plates, with food-to-plate diameter ratios: .47 (large food) and .32 (small food). C) **Delboeuf illusion condition** in which the same quantity of food, in this example canned tuna, was presented on a large and on a small white plastic plate of the same sizes as in the control conditions A) and B), respectively, with food-to-plate diameter ratios: .36 (large plate) and .47 (small plate). Note that each cat was tested with the same kind of food in all trials in all three conditions according to its food preference (details in Method).

### *Test Procedure*

Time of day of the tests depended on the owners' availability and was between 09:00 and 19:00 h. The cats were deprived of food for 4–6 h previously to motivate them to perform the task. Out of view from the owner and cat, the experimenter placed the appropriate stimuli (see Figure 1) on the plastic sheet, turned on the camera and walked to the farthest point at a right angle to the stimulus array. Staying aligned with the middle of the plastic sheet, the experimenter turned away from the experimental setup and remained motionless. The experimenter then asked the owner to come in carrying the cat. The owner placed the cat on the chair facing the stimuli, and gently held it there from behind for 5 seconds to give it the chance to view both plates before releasing it to make its choice. We defined "choice" as the cat going to one of the plates and manipulating the food (licking, eating or pawing). As soon as the cat chose a plate the experimenter removed the other plate and allowed the cat to eat briefly from the chosen stimulus. We only allowed brief eating to prevent the cats becoming satiated and losing motivation to participate in further trials. To avoid cueing the cats, neither the owner nor experimenter looked at the cat, instead focusing their attention straight ahead at the opposite wall until the cat made its choice (see video of typical trials in Supplementary Material Annex).



**Figure 7. Testing procedure.** The owner placed the cat on the chair facing the stimuli and without looking at the cat held it there from behind for 5 seconds to give it the chance to view both plates before releasing it to make its choice. The experimenter remained turned away and motionless until the cat chose a plate, then she removed the non-chosen plate and allowed the cat to eat briefly from the chosen stimulus.

Similar to previous studies with dogs and primates, the cats received a total of 48 trials across a minimum of eight days. Each daily session consisted in a maximum of six trials; two trials for each of the three conditions. If cats lost motivation (if they stopped making choices) during a session, we stopped testing for that day and continued testing on additional days until each cat had completed the full experimental program. In all cases we left at least one day between sessions. To control for possible side preferences (see Animals, Housing and Sample Sizes above), we counterbalanced the left-right presentation of the small/large plates and small/large portion of food for all cats across trials. We also reversed the location

of the stimuli in the test room in each session, and randomly assigned the order of presentation for each condition across sessions and subjects.

#### *Data Treatment and Statistical Analysis*

Statistical analyses were performed using R version 3.4.1 (R Core Team, 2017). For the analyses of individuals' performance, binomial tests were conducted on the proportion of choices for the larger quantity of food (control trials), and for the proportion of choices for the portion of food presented on the smaller plate (illusion trials). Population-level values were analyzed using parametric statistics as they were normally distributed (Shapiro–Wilk test,  $p > .05$ ; (Shapiro & Wilk, 1965). To assess whether the cats could discriminate between the two quantities in the two control conditions and select one plate more often than expected by chance in the illusion condition we performed one-sample Student's  $t$ -tests (two-tailed with chance level = .50) on the proportion of choices for the larger quantity of food in control trials and the proportion of choices for the food presented on the smaller plate in the illusion trials. Cohen's  $d$  values (Cohen, 1988) were calculated to estimate effect sizes. Comparisons of performance according to the animals' sex, whether they were neutered or intact, and whether they were exclusively indoor or indoor/outdoor pets, were done using Welch's  $t$ -test for unequal sample sizes (Welch, 1947). To assess correlations between individual cats' performance in the two control conditions, between their performance in the control and illusion conditions, and to check whether their performance changed with age and across trials we calculated Spearman's rank-order correlations (Spearman, 1904). A generalized linear mixed-effects model with binomial distribution (Nelder & Wedderburn, 1972) was used to compare performance among conditions (Large control/Small control/Illusion).

## RESULTS

A first question was whether the cats' performance during testing could have been influenced by the type of food presented. We found no difference in performance based on the type of food used (Fisher-Pitman permutation tests: canned food vs tuna  $p = .65$ , 95% CI [.64, .66]; canned food vs dry food  $p = .12$ , 95% CI [.11, .13]; tuna vs dry food  $p = .34$ , 95% CI [.33, .35]).

### *Control Trials*

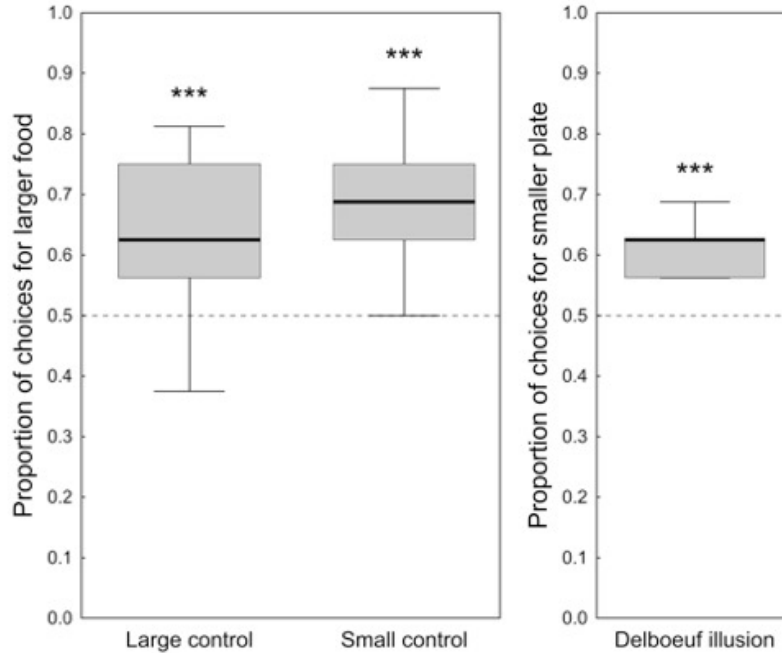
Cats chose the larger quantity of food more often in both control conditions. In the large-plate condition 14 of the 18 cats (78 %) chose the larger amount more often, three cats chose the larger and smaller amounts equally often, and one cat chose the smaller amount more often (see Table 1 in Annex). The cats' overall performance ( $M = .64$ , 95% CI [.58, .70]) was significantly above chance (one-sample Student's  $t$ -test:  $t(17) = 4.97$ ,  $p < .001$ ; Cohen's  $d = 1.17$ ), even though at the individual level only two of them reached significance (Table 1 in Annex). In the small-plate condition 15 of the 18 cats (83 %) chose the larger amount of food more often and the rest chose the larger and smaller amounts equally often. In this condition overall performance was also significantly above chance ( $M = .69$ , 95% CI [.63, .75];  $t(17) = 6.60$ ,  $p < .0001$ ; Cohen's  $d = 1.55$ ), although at the individual level only four of the cats reached significance (Table 1 in Annex). The low number of cats choosing the larger amount of food significantly above chance during the control trials might be explained by the low number of repetitions they were given for each of the two control conditions: with 16 repetitions each, a high number of "correct" choices (at least 13/16) is needed for the results to be significant. Nevertheless, when we combined the data from all the trials of the two control conditions, 9 of the 18 cats chose the larger amount of food significantly above chance according to the binominal test (Table 1 in Annex).

In addition, we found a significant positive correlation between individual cats' performance in the two control conditions (Spearman  $r_s = .46$ ,  $p < .05$ ), and no difference in overall performance in the two conditions (paired  $t$ -test  $t(17) = 1.74$ ,  $p = .10$ ). Thus, for

further analysis data from the two conditions were pooled. We found no difference in performance between sexes (Welch's  $t$ -test,  $t(13.51) = 0.03$ ,  $n_{\text{female}} = 8$ ,  $n_{\text{male}} = 10$ ,  $p = .97$ ), or between intact and neutered cats (Welch's  $t$ -test,  $t(15.99) = 1.03$ ,  $n_{\text{intact}} = 7$ ,  $n_{\text{neutered}} = 11$ ,  $p = .32$ ). However, we did find a difference according to the cats' living conditions. Overall, indoor/outdoor cats chose the larger food portion more often than exclusively indoor cats (72 % vs. 61 %, respectively; Welch's  $t$ -test,  $t(14.12) = 2.62$ ,  $n_{\text{indoor}} = 9$ ,  $n_{\text{outdoor}} = 9$ ,  $p < .05$ ). There was no correlation between age and overall performance (Spearman  $r_s = -.37$ ,  $p = .13$ ), which is consistent with previous findings for cats (Bánszegi et al., 2016) and dogs (Petrazzini et al., 2016; Ward & Smuts, 2007) on similar tasks. There was also no correlation between the overall percentage of cats that chose the larger stimulus in either of the control conditions and the order of the trials ( $r_s = -.21$ ,  $p = .43$ ), suggesting that there were no significant learning effects in the control trials during the study.

### *Illusion Trials*

In the Delboeuf illusion trials all 18 cats chose the food presented on the smaller plate more often than on the larger one ( $M = .62$ , 95% CI [.59, .65], Student's  $t$ -test:  $t(17) = 9.45$ ,  $p < .001$ , Cohen's  $d = 2.23$ ), which suggests that they were susceptible to the Delboeuf illusion; however, at the individual level none of them performed significantly above chance according to the binomial tests. We found no difference between sexes (Welch's  $t$ -test:  $t(13.4) = 0.76$ ,  $n_{\text{female}} = 8$ ,  $n_{\text{male}} = 10$ ,  $p = .46$ ), nor between cats that were reproductively intact or neutered ( $t(8.85) = 0.19$ ,  $n_{\text{intact}} = 7$ ,  $n_{\text{neutered}} = 11$ ,  $p = .85$ ), nor between exclusively indoor or indoor/outdoor pets ( $t(14) = 0.26$ ,  $n_{\text{indoor}} = 9$ ,  $n_{\text{outdoor}} = 9$ ,  $p = .80$ ). We found no correlation between age and performance (Spearman  $r_s = .001$ ,  $p = .99$ ), between overall performance in the control trials and performance in the illusion trials ( $r_s = -.32$ ,  $p = .20$ ), nor between the cats' performance in the illusion trials and the order of the tests ( $r_s = .32$ ,  $p = .22$ ), suggesting that there were no learning effects across the illusion trials.



**Figure 8.** Performance of the cats (N = 18) when tested in the two control conditions (left panel) and in the Delboeuf illusion condition (right). Solid horizontal lines give medians, boxes indicate 25th and 75th percentiles, and vertical lines show the minimum and maximum values. In all three conditions, performance was significantly above chance (horizontal dotted line, \*\*\*  $p < .001$ ), as reported by one-sample t tests (see Data Treatment and Statistical Analysis above).

Finally, we analysed whether the cats' performance differed between the control and illusion trials using a generalized linear mixed-effects model with binomial distribution that included the type of test and the individuals' living conditions (indoor or indoor/outdoor) since this was found to have an effect in the control trials. We found no difference in overall performance for the type of trials whereas living conditions had a significant effect on the number of "successful" trials (choice of the larger portion of food in the control trials, or the seemingly larger portion of food in the illusion trials was greater by indoor/outdoor cats), while the interaction of these two factors was not significant (GLMM trial:  $\chi^2 = 0.24$ ,  $p = .62$ , conditions:  $\chi^2 = 4.87$ ,  $p < .05$ , trial\*condition  $\chi^2 = 0.05$ ,  $p = .83$ ; summarizes individual performance of subjects).



## DISCUSSION

The results of the two control conditions (different quantities of food with a ratio of .44 in their surface area, presented on large or on small plates; Figure 6) confirm that with no prior training domestic cats distinguish between different quantities of food presented in a standardized experimental paradigm, and that they choose the larger amount above chance, at least at the group level. This result is consistent with previous findings on the domestic cat (Bánszegi et al., 2016). Despite this finding, at the individual level only two cats chose the larger amount of food significantly above chance in the large-plate condition and only four of them in the small-plate condition. However, when we combined the data from the two control conditions (since overall performance did not differ between the two), 50 % of cats demonstrated a preference for the larger amount of food significantly above chance at the individual level. Consistent with results from a previous study of quantity discrimination in cats (Bánszegi et al., 2016) and with reports for other carnivores (Baker et al., 2011; Petrazzini et al., 2016; Ward & Smuts, 2007), we also did not find a correlation between the overall performance of the cats in either of the control conditions and the order of the trials, suggesting that there were no significant learning effects during the study.

Adjusting the paradigm slightly to create (for human viewers, Figure 3) the Delboeuf illusion, we obtained the first suggestive evidence that cats, like humans (McClain et al., 2014; Van Ittersum & Wansink, 2012) and some non-human primates (Parrish & Beran, 2014; Parrish et al., 2015), are also susceptible to this illusion. When presented simultaneously with two equal quantities of a preferred food on a large and on a small plate, the cats, as a group, chose the food on the small plate significantly above chance, presumably because it appeared to be a larger quantity compared to the food on the large plate, even though no individual cat performed significantly above chance. This result can be explained by the fact that all cats chose the small plate more often (~ 62 %), and the standard deviation for the cats as a group was quite small, which resulted in a relatively large effect size. Furthermore, this was true even though the position of the two food stimuli (left/right) and their arrangement in the room was randomized across trials. Consistent with previous findings on

the judgment of food quantity by coyotes (Baker et al., 2011), dogs (Ward & Smuts, 2007), cats (Bánszegi et al., 2016) and rats (Wadhera et al., 2017), the animals of the present study must have made their choice based on visual cues alone; as the food portions in the illusion condition were of the same size, olfaction could not have played a part.

There has been relatively little comparative work on perception of visual illusions, including the Delboeuf illusion, across mammalian species, and so we aimed to make our methods comparable to at least some of the previous work in primates (Parrish & Beran, 2014; Santacà et al., 2017) and in the domestic dog (Petrazzini et al., 2016). While our results indicate that cats, like several non-human primates, perceive the Delboeuf illusion (Parrish & Beran, 2014; Parrish et al., 2015), they contrast with reports that the domestic dog apparently does not, and even if perhaps some individuals do so, in the opposite direction to humans, other primates and to the cats of the present study (Byosiére et al., 2017b; Petrazzini et al., 2016). Petrazzini and collaborators (2016) found that despite the dogs spontaneously discriminate between large and small amount of food and choose the larger amount above chance level, they did not discriminate between the food proportion if they are placed on different sized plates, meaning they did not perceive the illusion. In addition, Byosiére and collaborators (2017b) found that some of the dogs in a trained two-way choice test consistently showed a reversed susceptibility to the Delboeuf illusion compared to humans and non-human primates, meaning that from the two same size target circle they chose which was on a larger “plate”.

One possible explanation for the difference between the results for dogs and cats could be differences in experimental methodology. In one of the studies in the case of dogs, the experimenters tied the subject with a leash to the wall at a distance of approximately 1.5 m from a midline between the plates. The fact that experimenters chose to test the dogs from a floor level could have led to different-distorted views for the illusion stimuli taken into account that depending on the dog’s height, their perception might have changed (Petrazzini et al., 2016). Byosiére and collaborators (2017b) during their experiment used a wooden apparatus with a touchscreen monitor specifically designed for their study (called the Canine Nose-Touch Testing), implemented to reduce any experimenter-expectancy effect and to

decrease possible environmental distractions throughout the trials. The stimuli (the two control and the illusion trials) were presented on this touchscreen monitor. The screen was located at approximately the height of the dog's eyes. Below the screen, there was a remotely controlled treat dispenser that distributed one treat as positive reinforcement and above the monitor there was a video camera that recorded each trial. They also pre-trained the dogs approximately 4 months to get familiarized to the testing apparatus and to touch the screen with their nose while they make their choice.

In contrast with the above-mentioned canine studies, to reduce stress and increase concentration to perform the task, in the present study the cats were all tested in their home environment with an individually preferred food and, in addition, they were tested from an elevated starting position, not at floor level, so as to give them a clear, non-distorted view of the two stimuli. Moreover, we in our study the cats chose spontaneously between the two different stimuli without any prior training.

But perhaps more importantly, it is not clear whether the effective ratio of the difference in size between a target stimulus (e.g. food) and surround (e.g. plate size) on which the Delboeuf illusion depends differs across species since most have only been tested on few options (critique in Parrish et al., 2015). In the present study, following for comparative purpose Petrazzini et al. (2016), during the illusion trials the cats discriminated between food-to-plate diameter ratios of 0.5 (on the small plate) and 0.36 (on the large plate), preferring to choose the stimulus with a ratio of 0.5, where the rim of the plate bordered the food more closely. However, these ratios do not correspond to those found to be the most effective in producing the Delboeuf illusion in humans (reviewed in Nicolas, 1995). The first time Delboeuf presented the illusion, used a black disks measuring 28 cm in diameter that were drawn on a white surface; he esteemed for the illusion, that the ratio between the black dot and the white background has to be 3:2 for the maximum overestimation, and if the ratio continues to increase, approximately to 5:1 or to 6:1 the illusion will turn and humans will see the black disk smaller.

Thus, it is possible that by modifying these ratios, either by reducing the smaller of the two ratios (for example, by making the large plate larger) or increasing the larger ratio

(making the smaller plate smaller), the visual assimilation and/or contrast effects (Goto et al., 2007) would become stronger, and a corresponding shift would be observed in the results. For example, Parrish et al. (2015) found in a series of experiments that rhesus and capuchin monkeys were more susceptible to the Delboeuf illusion when tested with a smaller plate/target object ratio on the large plate and a larger plate/target object ratio on the small plate. Here researchers introduced a task in which monkeys classified eight different dot-to-ring ratios: 0 (no ring), 0.25, 0.33, 0.45, 0.50, 0.55, 0.67 and 0.75. They predicted that if the Delboeuf illusion was perceived, the underestimation of dot size would be most likely to occur at lower ratios ( $<0.50$ ) since these produced larger rings relative to the target dots and an overestimation of dot size (that is, subjects will perceive the illusion), would be most likely to occur at higher ratios as these produced smaller rings relative to the target dots ( $>.50$ ). They found that the ratios of 0.25 and 0.75 appeared to be most effective for monkeys and humans (Parrish et al., 2015).

While in the present study the cats appear to have perceived the Delboeuf illusion even with the ratios mentioned above, for future studies it remains a methodological concern to determine the most appropriate ratios. Thus, it may be that in some species such as dogs and lemurs reported not to perceive the Delboeuf illusion (Petrazzini et al., 2016; Santacà et al., 2017), that by modifying the ratios of the test stimuli, the animals become susceptible to it.

A compelling explanation for why some species are susceptible to the Delboeuf illusion but others are not is not yet available, although the differences in test design and methods could potentially contribute. For example, studies differ in whether they used spontaneous choice tests or (sometimes extensive) training. While spontaneous choice tasks can show how the animals behave in more naturalistic situations, studies using trained animals are useful for exploring the absolute perceptual or cognitive abilities of a species (Agrillo & Bisazza, 2014). Another methodological inconsistency is whether the subjects were tested with food-related or non-ecologically relevant stimuli (e.g. touch screens), and whether they were rewarded in the case of a particular choice, as both of these factors can influence the animals' motivation. In the present study we tested the cats in a spontaneous

choice task, with the aim of exploring their natural perceptual tendencies. Additionally, we tested them with food stimuli to make the test naturally relevant and to maintain a high level of motivation. Certainly, further systematic, investigation is required to explain divergent findings across studies, including the recruitment of other species with different evolutionary backgrounds and diverse sensory and perceptual characteristics.

A notable finding of the present study was the lack of correlation between individual performance in the control conditions and performance in the illusion condition; that is, individuals who were more accurate in choosing the larger item in the control trials did not necessarily show a correspondingly higher susceptibility to the Delboeuf illusion, even though at the group level the cats were susceptible. Since the sample size (and the tested ratios, both in the control and illusion conditions) was quite low we are limited in the ability to make this connection using the present data and must be cautious regarding the interpretation of this lack of correlation. Nevertheless, it might suggest a difference in the processing of visual information involved in size judgment in the presence or absence of a misleading surround. A possibility is that whereas size discrimination, uncomplicated by a distorting surround, depends mainly on peripheral, bottom-up mechanisms (this means, the chain of events begins with the external stimulus itself before progressing upwards through the various stages of mental processing, culminating in a visual experience [McLeod, 2018]), the perception of illusions is the product of more central, top-down processing (whereby information about what we are looking at travels down to the visual cortex from higher cortical regions, generating a visual experience that is internally created and is not a reflection of the real world [Gilbert & Li, 2013]), possibly dependent on continuing early maturational processes and/or experience gained during development. The utility of “top-down” cognition is that it allows the brain to fill in the gaps in our visual field by drawing on previous experiences and understanding of what the world should look like, generating the visual image that it expects to see. Generally, these two processes complement each other perfectly, although optical illusions demonstrate how easy is to trick the brain into something simply because it had already expected to see it, even if it is not actually there, creating

“feedback loops” that supplement the external stimuli seen by the eyes (Pafundo et al., 2016).

Consistent with such a possible perceptual disjunction, children under seven years of age are able to judge the size of a target object with great accuracy, but it is not until later in development that they become susceptible to the influence of misleading contexts creating visual illusions (Doherty et al., 2010; Káldy & Kovács, 2003; Parrish et al., 2016). Since illusion-mediating neural circuits probably involve higher cortical areas (Livingstone & Hubel, 1988), the connectivity which supports contextual sensitivity might not be fully developed at a younger age (Káldy & Kovács, 2003). This is consistent with the research of Poirel et al. (2011), that loss of grey matter in the right parietal and visual areas of children around six years of age may reflect anatomical maturation. Thus, lack of correlation between judgment of a target’s actual size and susceptibility to related illusions suggests that the perception of visual illusions and discrimination of actual size are processed by the nervous system differently. It is also possible that different illusions might invoke different underlying neural mechanisms as suggested by studies that tested the susceptibility to different illusions in the same individuals (Byosiére et al., 2017b; Song et al., 2011). In humans, for example, inter-individual variability in the strength of the perception of two illusions was not significantly correlated across participants (Schwarzkopf et al., 2011).

In a cross-cultural study, Fujita and collaborators (2017) found differences in the susceptibility to different illusions among people from different cultures, which suggests important contribution of prior experience or the so called “learning factor” to the illusory perception. In developmental studies, different visual illusions have been also found to follow different developmental courses. It is clear that visual illusions are not specific to human vision, which suggests an evolutionary background of this perceptual phenomenon favoured by apparently more efficient analyses of environmental stimuli by the system in regular encounters. Fujita and collaborators (2017) also suggest that visual illusions are a consequence of such adaptive adjustments, or limitations involved on the processing function of the visual system in inappropriate (or tricky) situations for the brain. Future research in which cats are tested with different types of visual illusions may help reveal

differences in the processing of visual information even compared, for example, to other Carnivora. Additionally, taking the cat as an experimentally accessible example, this also raises the question as to when during development kittens discriminate between, for example, different quantities of food, at what age they become susceptible to the Delboeuf illusion, and if there is a disjunction in developmental timing between the two?

## REFERENCES

1. Agrillo, C., & Bisazza, A. (2014). Spontaneous versus trained numerical abilities. A comparison between the two main tools to study numerical competence in non-human animals. *Journal of Neuroscience Methods*, *234*, 82-91. doi:10.1016/j.jneumeth.2014.04.027
2. American Pet Products Association. (2015). *APPA national pet owners survey 2015-2016*. Retrieved from [www.americanpetproducts.org](http://www.americanpetproducts.org)
3. Bååth, R., Seno, T., & Kitaoka, A. (2014). Cats and illusory motion. *Psychology*, *5*, 1131-1134. doi:10.4236/psych.2014.59125
4. Baker, J. M., Shivik, J., & Jordan, K. E. (2011). Tracking of food quantity by coyotes (*Canis latrans*). *Behavioural Processes*, *88*, 72-75. doi:10.1016/j.beproc.2011.08.006
5. Bánszegi, O., Urrutia, A., Szenczi, P., & Hudson, R. (2016). More or less: spontaneous quantity discrimination in the domestic cat. *Animal Cognition*, *19*, 879-888. doi:10.1007/s10071-016-0985-2
6. Bernstein, P. L. (2007). The human-cat relationship. In I. Rochlitz (Ed.), *The welfare of cats*. Springer, Netherlands. pp. 47-89
7. Blake, R. (1979). The visual system of the cat. *Perception & Psychophysics*, *26*, 423-448. doi:10.3758/BF03204283
8. Bradshaw, J. W. S., Casey, R. A., & Brown S. L. (2012). *The behaviour of the domestic cat*. 2<sup>nd</sup> edition, CABI Publishing, UK. pp. 27-36. doi: 10.1079/9781845939922.0001
9. Bradshaw, J. W. S., Goodwin, D., Legrand-Defretin, V., & Nott, H. M. R. (1996). Food selection by the domestic cat, an obligate carnivore. *Comparative Biochemistry and Physiology Part A: Physiology*, *114*, 205-209. doi:10.1016/0300-9629(95)02133-7
10. Bradshaw, J. W. S., Healey, L. M., Thorne, C. J., Macdonald, D. W., & Arden-Clark, C. (2000). Differences in food preferences between individuals and populations of domestic cats *Felis silvestris catus*. *Applied Animal Behaviour Science*, *68*, 257-268. doi:10.1016/S0168-1591(00)00102-7
11. Bravo, M., Blake, R., & Morrison, S. (1988). Cats see subjective contours. *Vision Research*, *28*, 861-865. doi:10.1016/0042-6989(88)90095-8
12. Byosiere, S. E., Chouinard, P. A., Howell, T. J., & Bennett, P. C. (2017a). What do dogs (*Canis familiaris*) see? A review of vision in dogs and implications for cognition research. *Psychonomic Bulletin & Review*, *25*, 1798-1813. doi:10.3758/s13423-017-1404-7



13. Byosiere, S. E., Feng, L. C., Woodhead, J. K., Rutter, N. J., Chouinard, P. A., Howell, T. J., & Bennett, P. C. (2017b). Visual perception in domestic dogs: susceptibility to the Ebbinghaus–Titchener and Delboeuf illusions. *Animal Cognition*, *20*, 435-448. doi:10.1007/s10071-016-1067-1
14. Cohen, J. (1988). *Statistical power analysis for the behavioral sciences*. 2<sup>nd</sup> edition. Hillsdale, NJ: Lawrence Erlbaum Associates.
15. Girgus, J. S., Coren, S., & Agdern, M. (1972). The interrelationship between the Ebbinghaus and Delboeuf illusions. *Journal of Experimental Psychology*, *95*, 453–455. doi:10.1037/h0033606
1. Davis, B., Payne, C. R., & Bui, M. (2016). Making small food units seem regular: how larger table size reduces calories to be consumed. *Journal of the Association for Consumer Research*, *1*, 115-124. doi:10.1086/684527
2. De Weerd, P., Vandenbussche, E., De Bruyn, B., & Orban, G. A. (1990). Illusory contour orientation discrimination in the cat. *Behavioural Brain Research*, *39*, 1-17. doi:10.1016/0166-4328(90)90117-W
3. Delboeuf, M. J. (1865). Seconde note sur de nouvelles illusions d’optique: essai d’une théorie psychophysique de la manière dont l’oeil apprécie les grandeurs. *Bulletins de l’Académie Royale des Sciences, Lettres et Beaux-arts de Belgique*, *20*, 70-97.
4. Delmar Cerutti, R., Rizzo, M., Alberghina, D., Cristina Scaglione, M., & Piccione, G. (2018). Locomotor activity patterns of domestic cat (*Felis silvestris catus*) modulated by different light/dark cycles. *Biological Rhythm Research*, *50*, 838-844. doi: 10.1080/09291016.2018.1499372
5. Doerr, N. R., & Endler, J. A. (2015). Illusions vary because of the types of decorations at bowers, not male skill at arranging them, in great bowerbirds. *Animal Behaviour*, *99*, 73-82. doi:10.1016/j.anbehav.2014.10.022
6. Doherty, M. J., Campbell, N. M., Tsuji, H., & Phillips, W. A. (2010). The Ebbinghaus illusion deceives adults but not young children. *Developmental Science*, *13*, 714-721. doi:10.1111/j.1467-7687.2009.00931.x
7. Driscoll, C. A., Macdonald, D. W., & O'Brien, S. J. (2009). From wild animals to domestic pets, an evolutionary view of domestication. *Proceedings of the National Academy of Sciences of the United States of America*, *106*, 9971-9978. doi:10.1073/pnas.0901586106
8. Eagleman, D. M. (2001). Visual illusions and neurobiology. *Nature Reviews Neuroscience*, *2*, 920-926. doi:10.1038/35104092
9. Feng, L. C., Chouinard, P. A., Howell, T. J., & Bennett, P. C. (2017). Why do animals differ in their susceptibility to geometrical illusions? *Psychonomic Bulletin & Review*, *24*, 262-276. doi:10.3758/s13423-016-1133-3

10. Fujita K., Nakamura, N., Watanabe, S. & Ushitani, T. (2017). Chapter 8. Comparative visual illusions: evolutionary, cross-cultural and developmental perspectives. In: *APA Handbook of Comparative Psychology; Volume 2, Perception, Learning and Cognition*. American Psychological Association. Washington, DC. 163-177. doi:10.1037/0000012-000
11. Gilbert, C., Li, W. (2013) Top-down influences on visual processing. *Nature Reviews Neuroscience*, *14*, 350-363. doi:10.1038/nrn3476
12. Girgus, J. S., Coren, S., & Agdern, M. (1972). The interrelationship between the Ebbinghaus and Delboeuf illusions. *Journal of Experimental Psychology*, *95*, 453-455. doi:10.1037/h0033606
13. Goto, T., Uchiyama, I., Imai, A., Takahashi, S., Hanari, T., Nakamura, S., & Kobari, H. (2007). Assimilation and contrast in optical illusions. *Japanese Psychological Research*, *49*, 33-44. doi:10.1111/j.1468-5884.2007.00330.x
14. Gregory, R. L. (1997). Visual illusions classified. *Trends in Cognitive Sciences*, *1*, 190-194. doi:10.1016/S1364-6613(97)01060-7
15. Griggio, M., Hoi, H., Lukasch, B., & Pilastro, A. (2016). Context-dependent female preference for multiple ornaments in the bearded reedling. *Ecology and Evolution*, *6*, 493-501. doi:10.1002/ece3.1903
16. Gunn-Moore, D., Moffat, K., Christie, L. A., & Head, E. (2007). Cognitive dysfunction and the neurobiology of ageing in cats. *Journal of Small Animal Practice*, *48*, 546-553. doi:10.1111/j.1748-5827.2007.00386.x
17. Heesy, C. P. (2008). Ecomorphology of orbit orientation and the adaptive significance of binocular vision in primates and other mammals. *Brain, Behavior and Evolution*, *71*, 54-67. doi:10.1159/000108621
18. Jaeger, T. (1978). Ebbinghaus illusions: size contrast or contour interaction phenomena? *Perception & Psychophysics*, *24*, 337-342. doi:10.3758/BF03204250
19. Káldy, Z., & Kovács, I. (2003). Visual context integration is not fully developed in 4-year-old children. *Perception*, *32*, 657-666. doi:10.1068/p3473
20. Kelley, L. A., & Kelley, J. L. (2014). Animal visual illusion and confusion: the importance of a perceptual perspective. *Behavioral Ecology*, *25*, 450-463. doi:10.1093/beheco/art118
21. Lamb, T. D., Collin, S. P., & Pugh, E. N. (2007). Evolution of the vertebrate eye: opsins, photoreceptors, retina and eye cup. *Nature Reviews Neuroscience*, *8*, 960-976. doi:10.1038/nrn2283
22. Livingstone, M., & Hubel, D. (1988). Segregation of form, color, movement, and depth: anatomy, physiology, and perception. *Science*, *240*, 740-749. doi:10.1126/science.3283936

23. Mascialzoni, E., & Regolin, L. (2011). Animal visual perception. *Wiley Interdisciplinary Reviews: Cognitive Science*, 2, 106-116. doi:10.1002/wcs.97
24. Masland, R. H., & Martin, P. R. (2007). The unsolved mystery of vision. *Current Biology*, 17, R577-R582. doi:10.1016/j.cub.2007.05.040
25. McClain, A. D., van den Bos, W., Matheson, D., Desai, M., McClure, S. M., & Robinson, T. N. (2014). Visual illusions and plate design: the effects of plate rim widths and rim coloring on perceived food portion size. *International Journal of Obesity*, 38, 657-662. doi:10.1038/ijo.2013.169
26. McLeod, S. A. (2018). Visual perception theory. Simply psychology. Retrieved from <https://www.simplypsychology.org/perception-theories.html>
27. Miller, P. E., & Murphy, C. J. (1995). Vision in dogs. *Journal of the American Veterinary Medical Association*, 207, 1623-1634.
28. Mitchel, D. L. M. (1971). *Cat visual response to certain geometric illusions* (Master thesis). McMaster University Hamilton, Ontario. 1-23. Retrieved from: [https://macsphere.mcmaster.ca/bitstream/11375/20909/1/Mitchell\\_Donna\\_L\\_M\\_1971\\_09\\_master.pdf](https://macsphere.mcmaster.ca/bitstream/11375/20909/1/Mitchell_Donna_L_M_1971_09_master.pdf)
29. Møller, A. P. (2017). Experimental manipulation of size and shape of tail spots and sexual selection in barn swallows. *Current Zoology*, 63, 569–572. doi:10.1093/cz/zow098
30. Mruczek, R. E. B., Blair, C. D., Strother, L., & Caplovitz, G. P. (2017). Size contrast and assimilation in the Delboeuf and Ebbinghaus illusions. In A. G. Shapiro & D. Todorović (Eds.), *The Oxford compendium of visual illusions* (1st ed.). Oxford University Press, UK . 262-274
31. Murphy, M., Lusby, A. L., Bartges, J. W., & Kirk, C. A. (2012). Size of food bowl and scoop affects amount of food owners feed their dogs. *Journal of Animal Physiology and Animal Nutrition*, 96, 237-241. doi:10.1111/j.1439-0396.2011.01144.x
32. Navon, D. (1977). Forest before trees: the precedence of global features in visual perception. *Cognitive Psychology*, 9, 353-383. doi:10.1016/0010-0285(77)90012-3
33. Nelder, J., & Wedderburn, R. (1972). Generalized Linear Models. *Journal of the Royal Statistical Society. Series A (General)*, 135, 370-384. doi:10.2307/2344614
34. Nicolas, S. (1995). Joseph Delboeuf on visual illusions: a historical sketch. *The American Journal of Psychology*, 108, 563-574. doi:10.2307/1423073
35. Oyama, T. (1960). Japanese studies on the so-called geometrical-optical illusions. *Psychologia*, 3, 7-20.

36. Pafundo, D.E., Nicholas, M. A., Zhang, R. & Kuhlman, S. J. (2016). Top-down-mediated facilitation in the visual cortex is gated by subcortical neuromodulation. *Journal of Neuroscience*, *36*, 2904-2914. doi: 10.1523/JNEUROSCI.2909-15.2016
37. Parker, M., Lamoureux, S., Challet, E., Deputte, B., Biourge, V., & Serra, J. (2019). Daily rhythms in food intake and locomotor activity in a colony of domestic cats. *Animal Biotelemetry*, *7*, 1-14. doi: 10.1186/s40317-019-0188-0
38. Parrish, A. E., Agrillo, C., Perdue, B. M., & Beran, M. J. (2016). The elusive illusion: do children (*Homo sapiens*) and capuchin monkeys (*Cebus apella*) see the Solitaire illusion? *Journal of Experimental Child Psychology*, *142*, 83-95. doi:10.1016/j.jecp.2015.09.021
39. Parrish, A. E., & Beran, M. J. (2014). When less is more: like humans, chimpanzees (*Pan troglodytes*) misperceive food amounts based on plate size. *Animal Cognition*, *17*, 427-434. doi:10.1007/s10071-013-0674-3
40. Parrish, A. E., Brosnan, S. F., & Beran, M. J. (2015). Do you see what I see? A comparative investigation of the Delboeuf illusion in humans (*Homo sapiens*), rhesus monkeys (*Macaca mulatta*), and capuchin monkeys (*Cebus apella*). *Journal of Experimental Psychology: Animal Learning and Cognition*, *41*, 395-405. doi:10.1037/xan0000078
41. Petrazzini, M. E. M., Bisazza, A., & Agrillo, C. (2016). Do domestic dogs (*Canis lupus familiaris*) perceive the Delboeuf illusion? *Animal Cognition*, *20*, 1-8. doi:10.1007/s10071-016-1066-2
42. Piccione, G., Marafioti, S., Giannetto, C., Panzera, M., & Fazio, F. (2013). Daily rhythm of total activity pattern in domestic cats (*Felis silvestris catus*) maintained in two different housing conditions. *Journal of Veterinary Behavior*, *8*, 189-194. doi:10.1016/j.jveb.2012.09.004
43. Pisa, P. E., & Agrillo, C. (2009). Quantity discrimination in felines: a preliminary investigation of the domestic cat (*Felis silvestris catus*). *Journal of Ethology*, *27*, 289-293. doi:10.1007/s10164-008-0121-0
44. Poirel, N., Simon, G., Cassotti, M., Leroux, G., Perchey, G., Lanoë, C., . . . Houdé, O. (2011). The shift from local to global visual processing in 6-year-old children is associated with grey matter loss. *PLoS ONE*, *6*, e20879. doi:10.1371/journal.pone.0020879
45. Randall, W., Johnson, R. F., Randall, S., & Cunningham, J. T. (1985). Circadian rhythms in food intake and activity in domestic cats. *Behavioral Neuroscience*, *99*, 1162-1175. doi: 10.1037//0735-7044.99.6.1162
46. Révész, G. (1924). Experiments on animal space perception. *British Journal of Psychology. General Selection*, *14*, 387-414. Doi: 10.1111/j.2044-8295.1924.tb00151.x
47. R Core Team. (2017). R: A language and environment for statistical computing (Version 3.4.1). Vienna, Austria. Retrieved from [www.R-project.org](http://www.R-project.org)

48. Santacà, M., Regaiolli, B., Petrazzini, M. E. M., Spiezio, C., & Agrillo, C. (2017). Preliminary study to investigate the Delboeuf illusion in ring-tailed lemurs (*Lemur catta*): methodological challenges. *Animal Behavior and Cognition*, *4*, 365-377. doi:10.26451/abc.04.03.13.2017
49. Schwarzkopf, D. S., Song, C., & Rees, G. (2011). The surface area of human V1 predicts the subjective experience of object size. *Nature Neuroscience*, *14*, 28–30. doi:10.1038/nn.2706
50. Shapiro, S. S., & Wilk, M. B. (1965). An analysis of variance test for normality (complete samples). *Biometrika*, *52*, 591-611. doi:10.1093/biomet/52.3-4.591
51. Song, C., Schwarzkopf, D. S., & Rees, G. (2011). Interocular induction of illusory size perception. *BMC Neuroscience*, *12*, 1-9. doi:10.1186/1471-2202-12-27
52. Spearman, C. (1904). The proof and measurement of association between two things. *The American Journal of Psychology*, *15*, 72-101. doi:10.2307/1412159
53. Traquair, Harry Moss (1938). An Introduction to Clinical Perimetry. *Kimpton Publisher*, London. pp. 4–5.
54. Turner, D. C., & Bateson, P. (2014). *The domestic cat: the biology of its behaviour*. 3<sup>rd</sup> edition, Cambridge University Press, UK. pp. 30
55. Van Ittersum, K., & Wansink, B. (2012). Plate size and color suggestibility: the Delboeuf Illusion's bias on serving and eating behavior. *Journal of Consumer Research*, *39*, 215-228. doi:10.1086/662615
56. Veilleux, C. C., & Kirk, E. C. (2014). Visual acuity in mammals: effects of eye size and ecology. *Brain, Behavior and Evolution*, *83*, 43-53. doi:10.1159/000357830
57. Vitale Shreve, K. R., & Udell, M. A. R. (2015). What's inside your cat's head? A review of cat (*Felis silvestris catus*) cognition research past, present and future. *Animal Cognition*, *18*, 1195-1206. doi:10.1007/s10071-015-0897-6
58. Wade, N. J. (2017). Early history of illusions. In A. G. Shapiro & D. Todorović (Eds.), *The Oxford compendium of visual illusions*. Oxford University Press, US. pp. 3-37
59. Wadhera, D., Wilkie, L. M., & Capaldi-Phillips, E. D. (2017). The rewarding effects of number and surface area of food in rats. *Learning & Behavior*, *46*, 242-255. doi:10.3758/s13420-017-0305-y
60. Wansink, B., & Van Ittersum, K. (2013). Portion size me: plate-size induced consumption norms and win-win solutions for reducing food intake and waste. *Journal of Experimental Psychology: Applied*, *19*, 320-332. doi:10.1037/a0035053
61. Ward, C., & Smuts, B. B. (2007). Quantity-based judgments in the domestic dog (*Canis lupus familiaris*). *Animal Cognition*, *10*, 71-80. doi:10.1007/s10071-006-0042-7

62. Wayne, R. K., Benveniste, R. E., Janczewski, D. N. & O'Brien, S. J. (1989) Molecular and biochemical evolution of the Carnivora. In: *Carnivore behaviour, ecology and evolution* (Gittleman JL, ed), pp. 465-494. Ithaca, N.Y: Cornell.
63. Welch, B. L. (1947). The generalization of "Student's" problem when several different population variances are involved. *Biometrika*, 34, 28-35. doi:10.1093/biomet/34.1-2.28
64. Williams, R. W., Cavada, C. & Reinoso-Suárez, F. (1993). Rapid evolution of the visual system: a cellular assay of the retina and dorsal lateral geniculate nucleus of the Spanish wildcat and the domestic cat. *The Journal of Neuroscience*, 13, 208-228. doi:10.1523/JNEUROSCI.13-01-00208.1993

## ANNEX

Table 1. Number of times each cat chose the larger portion of food in the two control conditions, in the two control conditions overall (pooled), and the smaller plate in the Delboeuf illusion condition (seemingly larger portion according to the illusion). *P* values refer to the results of testing each cat's choices against chance as reported by binomial tests. Conditions when choices were significantly different from chance ( $p < .05$ ) are boldfaced.

Cat name	Sex	Age (years)	Sexual status	Living condition	Large control	Small control	Overall control	Delboeuf illusion
Balam	M	7	Neutered	Indoor	9 / 16 <i>p</i> = .80	12 / 16 <i>p</i> = .08	21 / 32 <i>p</i> = .11	9 / 16 <i>p</i> = .80
Chufi	F	3	Neutered	Indoor	8 / 16 <i>p</i> = 1	11 / 16 <i>p</i> = .21	19 / 32 <i>p</i> = .38	10 / 16 <i>p</i> = .45
Crazy	F	3	Neutered	Indoor	10 / 16 <i>p</i> = .45	9 / 16 <i>p</i> = .80	19 / 32 <i>p</i> = .38	9 / 16 <i>p</i> = .80
Darcy	M	3	Intact	Outdoor	11 / 16 <i>p</i> = .21	<b>14 / 16</b> <i>p</i> = .004	<b>25 / 32</b> <i>p</i> < .01	9 / 16 <i>p</i> = .80
Erick	M	2.5	Intact	Outdoor	10 / 16 <i>p</i> = .45	<b>13 / 16</b> <i>p</i> = .02	<b>23 / 32</b> <i>p</i> < .05	10 / 16 <i>p</i> = .45
Gigi	F	2	Neutered	Indoor	12 / 16 <i>p</i> = .08	<b>14 / 16</b> <i>p</i> = .004	<b>26 / 32</b> <i>p</i> < .001	10 / 16 <i>p</i> = .45
Grafit	F	4	Neutered	Outdoor	<b>13 / 16</b> <i>p</i> = .02	<b>13 / 16</b> <i>p</i> = .02	<b>26 / 32</b> <i>p</i> < .001	10 / 16 <i>p</i> = .45
Hendri	M	1.5	Neutered	Outdoor	<b>13 / 16</b> <i>p</i> = .02	11 / 16 <i>p</i> = .21	<b>24 / 32</b> <i>p</i> < .01	10 / 16 <i>p</i> = .45
Ivy	F	1	Intact	Outdoor	10 / 16 <i>p</i> = .45	12 / 16 <i>p</i> = .08	<b>22 / 32</b> <i>p</i> = .05	12 / 16 <i>p</i> = .08
Lilith	F	1	Intact	Outdoor	12 / 16 <i>p</i> = .08	12 / 16 <i>p</i> = .08	<b>24 / 32</b> <i>p</i> < .01	9 / 16 <i>p</i> = .80

Lolo	M	6	Neutered	Indoor	6 / 16 <i>p</i> = .45	8 / 16 <i>p</i> = 1	14 / 32 <i>p</i> = .6	11 / 16 <i>p</i> = .21
Misifustófeles	M	3	Neutered	Indoor	11 / 16 <i>p</i> = .21	10 / 16 <i>p</i> = .45	21 / 32 <i>p</i> = .11	11 / 16 <i>p</i> = .21
Pancho	M	6	Neutered	Indoor	11 / 16 <i>p</i> = .21	8 / 16 <i>p</i> = 1	19 / 32 <i>p</i> = .38	10 / 16 <i>p</i> = .45
Pinky	F	3	Neutered	Indoor	8 / 16 <i>p</i> = 1	8 / 16 <i>p</i> = 1	16 / 32 <i>p</i> = 1	10 / 16 <i>p</i> = .45
Quetzalcóatl	M	2	Intact	Indoor	10 / 16 <i>p</i> = .45	10 / 16 <i>p</i> = .45	20 / 32 <i>p</i> = .29	10 / 16 <i>p</i> = .45
Shiro	M	2	Intact	Outdoor	12 / 16 <i>p</i> = .08	11 / 16 <i>p</i> = .21	<b>23 / 32</b> <b><i>p</i> &lt; .05</b>	9 / 16 <i>p</i> = .80
Solange	M	1.5	Neutered	Outdoor	10 / 16 <i>p</i> = .45	12 / 16 <i>p</i> = .08	<b>22 / 32</b> <b><i>p</i> &lt; .05</b>	9 / 16 <i>p</i> = .80
Zumba	F	2	Intact	Outdoor	8 / 16 <i>p</i> = 1	10 / 16 <i>p</i> = .45	18 / 32 <i>p</i> = .59	11 / 16 <i>p</i> = .21

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