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VISUAL COGNITION IN DOGS MOTION PERCEPTION

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to my parents

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SUMMARY

In the last decades several studies have been investigated the behavior and cognition of dogs (*Canis familiars*) especially from socio-cognitive aspects. We already gained a solid knowledge on how dogs communicate with humans and conspecific partners, how they are able recognize, interpret and rely on social-communicational cues in their everyday lives, thus continuously perceiving a flow of visual information. However, the fundaments of how they process these visual information are still missing from the literature. The current PhD project have been developed around three independent studies, all of them investigating visual cognition in dogs (and for one case, also in humans) in the domain of perceiving motion.

The ability to perceive motion is one of the main properties of the visual system. Sensitivity in detecting coherent motion has been thoroughly investigated in humans, where thresholds for motion detection are well below 10% of coherence, i.e. of the proportion of dots coherently moving in the same direction, among a background of randomly moving dots. Equally low thresholds have been found in other species, including monkeys, cats and seals. Given the lack of data from the domestic dog, in the first study we tested 5 adult dogs on a conditioned discrimination task with random dot displays. In addition, five adult humans were tested in the same condition for comparative purposes. We found that the mean threshold for motion detection in our dogs was 42% of coherence, while in humans we found it as low as 5%. Therefore, according to our first study dogs have a much higher threshold of coherent motion detection than humans, and possibly also than phylogenetically closer species that have been tested in similar experimental conditions. Since various factors, including

parameters of visual stimuli and experience related changes in visual perception might have played a role in these findings we developed additional studies for further investigation.

In the second study we aimed to investigate whether dogs' performance is sensitive to changes of dot density and dot lifetime of the stimuli, together with investigating whether repeated encounter with a specific visual pattern could result in experience related perceptual improvement in dogs by triggering the mechanisms of perceptual learning in the subjects. For this aim we conducted experiments with random dot displays in a two-way conditioned discrimination task, in which we systematically manipulated appropriate features of the stimuli and re-assessed our subjects' threshold after extensive exposure to the visual pattern. We found that both the decrease of dot density and dot lifetime took an effect on dogs' performance by decreasing the percentage of correct choices of the individuals. Moreover, our results suggest that perceptual learning is present in dogs, as 4 out of our 5 subjects showed a lowered threshold of detecting coherent motion after repeated encounters with the stimuli.

In the third study we investigated another aspect of the mechanisms of motion detection in dogs by measuring their motion speed thresholds that provides the ability of being able to discriminate static and moving visual patterns. For this aim we tested 4 adults pet dogs in two-way discrimination tasks. In line with our previous studies, we used random dot displays as visual patterns to discriminate. Our reference stimulus was a static image of dots while our moving stimulus were random dot displays where dot speed has been manipulated for assessing the lowest speed at which individuals could discriminate the static stimuli from the moving one with 80% accuracy. We found that

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dogs threshold for detecting movement is varying between 0.4 deg/s and 1.5 deg/s of speed, which results are similar to what is reported in human adults (0.4 deg/s) and in children (1 deg/s) however, much lower than what has been found in pigeons (4 deg/s).

CHAPTER 1

General introduction

The ability of perceiving coherent motion is one of the primal features of the visual system that started to emerge early in evolution (Ghering, 2012). Through domestication and facing challenges while adapting to the human environment, dogs earned to become one of the most promising model species to investigate human cognition from a comparative and evolutionary aspect (Miklosi et al., 2004). While physiological and socio-cognitive mechanisms, together with the fundaments of dogs' vision and their ability to use visual cues, have been deeply investigated, to the best of our knowledge, the only study reporting data on dogs' sensitivity for motion perception dates back to the first half of the 20th century.

According to several reports of the last decades, dogs own a special ability to recognize, interpret and use visual information for accurate communication with human partners. Such communicational signals involve pointing, gazing, bowing (Hare and Tomasello 1999; Soproni et al. 2001), as well as subtle human facial expressions that are also proved to be interpreted by dogs as visual cues (Kis et al., 2017; Buttelman and Tomasello, 2013). Beside these there are only a handful of behavioral studies which investigated fundamental abilities of dogs' visual system and revealed that dogs are able to discriminate global and local features of static visual patterns (Pitteri et al., 2014) and they have the ability to discriminate biological- from non-biological motion (Kovacs et al., 2016).

Being able to identify preys, and predators can make a difference in the survival ratio of the individual, thus the ability of detecting movement is one of the primal features of the visual system that started to emerge early in evolution (Ghering, 2012). Perceiving coherent motion is provided by the visual system through detecting units of local motion signals and integrating them over space and time (Braddick, 1993; Williams and Brannan, 1994). This phenomenon is commonly investigated by discrimination tasks of random-dot displays (Newsome and Pare, 1988), where a visual pattern of a given number of motion units (e.g. dots) are coherently moving in the same direction (signal), among dots moving in random directions (noise). The smaller the proportion of signal dots, that needed to allow the subject to perceive coherent motion, the lower is the individual's threshold of detecting coherent motion.

Since, as mentioned above, the sensation of coherent motion is a result of the integration of local motion units (Braddick, 1974; 1993) it is evident that the more energy (e.g. density and lifetime) a visual stimulus have, the more source of information the visual system can integrate, the earlier it is able to detect coherence in motion. Accordingly, the number of local motion units (dot density) and the time each unit's path is visible (dot lifetime) are crucial parameters of the visual stimulus and it has been proven that manipulating these parameters can notably effect coherent motion detection thresholds in both human and non-human subjects (Talcott et al., 2000; Snowden and Kanavagh, 2006; Weiffen et al., 2014).

Another factor that is possibly modifying individuals' performance in visual discrimination tasks is the effect of perceptual learning. This cognitive mechanism is an experience-dependent perceptual improvement, enabled by the plasticity of the visual system (Zohary et al., 1994; Gilbert, 1996). It consists of the ability of rapid adaptation

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to the continuously changing environment and triggered by frequent encounters with certain visual stimuli (Karni and Sagi, 1993; Watanabe et al., 2001). In the last decades this phenomenon has been widely investigated in adult humans over various visual tasks and reported to improve the performance of the subjects in texture (Karni and Sagi, 1991) and motion discrimination (Liu and Vaina, 1998) as well as coherent motion detection in humans, mice, monkeys and seals (Britten et al., 1992; Watanabe et al., 2001; Douglas et al., 2006; Weiffen, 2014). However, it has not yet been investigated whether perceptual learning is present in dogs nor their ability of being able to discriminate a stationary from a moving visual pattern that is crucial for adaptive behavior.

Hodos and coauthors (1976) studied threshold of speed discrimination in pigeons and reported that the lowest speed at which the subjects were able to discriminate a stationary from a moving visual stimulus varied between 4.1 and 6.1 deg/s (Hodos et al., 1976). Conversely, a more recent study that compared speed thresholds in human adults and 5 years old children found that adults need at least 0.4 deg/s speed difference between two visual stimuli to be able to discriminate them, while 5 years old children show a higher threshold of 1.1 deg/s which suggests that the system, underlying the mechanisms of this specific aspect of motion perception might be immature at the age of 5 years (Ahmed, 2006). Additional studies (Ellenberg et al., 2004; Aslin and Shea, 1990) are supporting this theory thus reporting velocity thresholds to be at approximately 9 deg/s in 6 weeks old infants that is dropping to 4 deg/s at the age of 12 weeks.

Aiming for a better and more complex understanding of the mechanisms that underlines dogs' visual cognition and deepening our knowledge on the characteristics of motion

perception, we aimed to study the characteristics of motion perception in dogs, through assessing their thresholds for coherent motion and movement detection, while directly comparing their ability of coherent motion detection with humans. In addition, we investigated which particular features of the visual stimuli could affect the performance of the subjects and whether perceptual learning occurs in dogs.

CHAPTER 2

Are dogs better than humans in detecting motion?

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INTRODUCTION

Perceiving motion, as one of the main properties of the visual system, is among the first features of visual abilities that started to develop through evolution (Ghering, 2014). The detection of movement in the environment is crucial for adaptive behavior, such as recognizing predators and preys. Sensitivity to coherent motion has led to a large body of research in various non-human species, as well as in different populations of humans. The perception of coherent motion starts with the detection and processing of information from several local motion units, enabling the perceptual system to build the representation of speed and direction of global motion (Borst & Euler, 2011). Individuals' sensitivity in the perception of coherent motion is typically assessed by the use of random-dot displays (Newsome & Pare, 1988), visual stimuli composed of a certain number of dots coherently moving in the same direction (signal dots), among dots moving in random directions (noise dots). The lower the proportion of signal dots in the display, the harder it is to discriminate the latter from displays composed only of noise dots. Detection thresholds are defined as the minimum proportion of coherently moving dots that allows a subject to reliably discriminate (with an arbitrarily chosen accuracy, generally set at 75%) the stimulus containing signal dots from a pure noise stimulus. Thus, in experimental procedures the proportion of signal dots is systematically varied, and detection accuracy is used to compute individual psychometric curves and thresholds as a function of the proportion of signal dots. The lowest thresholds reported for humans are well under 10% of coherence, although some variability exists across studies, possibly due to methodological differences (Talcott et al., 2000; Johnston et al., 2016). Similarly, low thresholds have also been reported for several non-human species, including monkeys (Newsome & Pare, 1988), cats (Huxlin & Pasternak, 2004; Rudolph & Pasternak, 1996) and seals (Weiffen et al., 2014). Higher thresholds, in the range of 20% to 60%, are reported for other species, such as pigeons (Bishof et al., 1999), rats and mice (Douglas et al., 2006). Higher thresholds are also found in specific human populations, such as children (Kassaliete et al., 2015; Parrish et al., 2005; Narasimhan & Giashi, 2012) adults with autism (Manning et al., 2015) or dyslexia (Talcott et al., 2000; Johnston et al., 2016).

Due to their history of domestication and convergent evolution with humans, dogs have faced challenges of adapting to the human environment, which makes them one of the most compelling species to investigate human cognition from a comparative aspect. Accordingly, in the last decades several studies have investigated dogs' abilities of using visual cues and reported that dogs have a special ability to use visual cues in communicating with humans, involving pointing, looking, bowing (Hare & Tomasello, 2005; Soproni et al., 2001), as well as relying on complex and subtle visual cues of emotional facial expressions (Buttelmann & Tomasello, 2013). Beside these studies on cognitive mechanisms underlying the dogs' ability to use visual cues, few behavioral studies looked at more basic functions of dogs' visual system and have revealed that dogs are able to discriminate global and local features of static visual stimuli (Pitteri et al., 2014) and to discriminate biological- from non-biological motion (Kovacs et al., 2015). However, to the best of our knowledge, studies about sensitivity of detecting coherent motion in dogs are lacking.

From a physiological point of view, the fundaments of dogs' vision have been deeply investigated. Most of the differences in visual perception between dogs and humans have been attributed to structural differences of the retina, and particularly in the number, distribution and neural connections of retinal photoreceptors, rods and cones (Peichl, 1992; Miller & Murphy, 1995; McGreevy et al., 2004). On the one hand, a lower concentration of cones in the central area of the retina and a higher degree of convergence of these photoreceptors on ganglion cells justifies a visual acuity 4 to 7 times lower in dogs than in humans (Miller & Murphy, 1995). Indeed, some findings indicate that such lower acuity is due to the structure of the retina and not to other optical properties of the eyes or post-retinal processing (Odom et al., 1983). On the other hand, a higher number of rods, and their more homogeneous distribution, including the area centralis of the retina (which completely lack rods in humans), contributes to dogs' higher sensitivity to light and an advantage over humans to see under dim light conditions. Interestingly, rods are also the photoreceptors primarily implied in the perception of motion; thus, the high number of rods in canine's retina has been suggested to play a part in dogs claimed high sensitivity towards moving stimuli (Miller & Murphy, 1995). However, to the best of our knowledge, the only study investigating dogs' sensitivity to moving targets dates back to the first half of the 20th century (Miller & Murphy, 1995), and no effort has been made in more recent times to replicate those findings, or to further investigate dogs' ability to detect coherent motion, neither per se nor from a comparative standpoint.

On these bases, we aimed to investigate the sensitivity of dogs for detecting coherent motion, using random dot displays in a two-way conditioned discrimination procedure. In addition, for a direct comparison with dogs, we investigated adult humans' thresholds of perception of coherent motion, in the same experimental conditions (i.e. with stimuli having the same parameters of size, density and speed and a similar assessment protocol) of our dogs.

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METHODS

Subjects

Dogs

Our sample was comprised of five pet dogs, three females and two males, between 3 and 11 years of age. The sample included one dog for each of the following breeds: Cocker Spaniel, Golden Retriever, Labrador-Poodle mix ('Labradoodle'), Mudi, and Siberian Husky. The owners were all workers and students of the University of Padova and participated in the experiments on a voluntary basis. All subjects underwent a veterinary examination before being enrolled in the tests and did not have any health conditions that would prevent them from participation. Dogs were selected according to high motivation for food and the willingness to cooperate and feel comfortable with being in the laboratory.

Humans

Our sample comprised five volunteers, three females and two males, between 25 and 45 years of age. Subjects were selected on the criterion that they were not familiar with stimuli and task.

Stimuli

Stimuli were created with MATLAB (MATLAB version 7.10.0. Natick, Massachusetts: The MathWorks Inc., 2010), using features of Psycho Toolbox (Brainhard, 1997; Pelli, 1997). The stimuli were shown on a black squared area of 31.1 x 31.1 cm (24.0 x 24.0 deg, from the viewing distance of 70 cm), where white dots with a diameter of 0.16 cm moved at a speed of 19.4 cm/s (15.0 deg/s). Each dot had a lifespan of 1 s, after which it disappeared and was regenerated in a different part of the display. There was a total of 5000 dots moving in the display, for a density of 5.9 dots / cm^{2} (8.7 dots/deg²). Dot size, density and speed were chosen based on stimuli that were previously used for testing other species in similar experiments (Weiffen et al., 2014; Brainhard, 1997), and, for dot size, also on known physiological values of visual acuity in dogs (Miller & Murphy, 1995). For the training phase, the target stimulus was set at a coherence of 80%, i.e. 80% of the dots moved in the same direction (towards the left side of the display), whereas the remaining 20% moved in random directions. In the test phase (see below), subjects were presented with a set of target stimuli with five levels of coherence (varied within blocks). For dogs these were 60%, 50%, 40%, 30% and 20%; for humans they were 30%, 20%, 5%, 2.5% and 1%. The levels of coherence for the test stimuli were created in accordance with previous studies in both human and non-human species (Weifen et al., 2014; Bishof et al., 1999; Brainhard, 1997). The non-target stimulus had a coherence level of 0%, that is all of the dots moved in random directions, in all trials of the training and test phase.

Experimental setting

All the experiments took place in the Laboratory of Applied Ethology of the Department Biomedicine and Food Science (University of Padova), in a testing area of 2.5 x 3 m. Stimuli were presented on two identical monitors (VG248QE, ASUSTeK Computer Inc., Taipei, Taiwan), whose refresh rate was set at 120 Hz; this setting was meant to prevent possible biases on dogs' detection of motion, due to their higher flicker fusion frequency²¹. Monitors had touch-screen capabilities, so touches of their surface (i.e. choices of either stimulus, as detailed below) were automatically recorded. Monitors were connected to a PC (Optiplex 960, Dell Inc., Round Rock, Texas, USA). Monitors were placed 25 cm away from each other, on two height-adjustable stands, so their height could be set at eye level for each subject. Presentations were controlled with a Bluetooth keyboard (Logitech).

Procedure for dogs

General trial procedure

Initially, dogs underwent a preliminary phase, in which they were shaped to touch the screen with the nose and got accustomed to the trial procedure. During each trial, subjects were standing or sitting beside the experimenter who held the dog gently by its harness, within a marked area at 75 cm from the monitors. When the dog was oriented toward the monitors, the experimenter closed her eyes to avoid influencing the subjects' choice and started the presentation of the stimuli. The non-target and the target stimuli appeared, one on each monitor, and remained visible until subject's

response. The experimenter held the dog for 4 seconds then said "Go!", let the subject free to choose one of the two stimuli, which the dogs did by touching the monitor with the nose. The experimenter reopened her eyes as soon as the dog moved towards the monitors. If the dog chose the target stimulus, the experimenter gave verbal and food reward to the dog, then called it back into the starting position. If the dog chose the non-target stimulus, the experimenter called it back into the starting position without giving any reward.

Training phase

This phase was aimed at training dogs to discriminate a stimulus with a high percentage of coherently moving dots from a stimulus of randomly moving dots. Dogs underwent sessions of 20 consecutive trials, as described above. In each trial, the non-target (0% coherence) and the target stimulus (80% coherence) were presented. The side of presentation of the two stimuli was randomly chosen by the software and balanced within the 20 trials. Each dog underwent a maximum of 5 training sessions per day, with an interval between session of at least 20 minutes. Dogs were only fed at the end of the day, in the days in which they were involved in the study. Subjects could proceed to the subsequent test phase when they chose the target stimulus for at least 18 out of 20 trials (i.e. 90% accuracy) in 6 consecutive sessions, distributed over two separate days.

Test phase

This phase was meant to assess dogs' threshold of perception of coherent motion. Sessions of this phase were composed of 24 trials. In the first 4 trials, dogs were presented with the same stimuli as those of the training phase (80% coherence), as a 'warm-up'; another 10 of such training trials were randomly interposed with others among the rest of the session. Inclusion of these training trials in the test session aimed at maintaining dogs' motivation and at further controlling the maintenance of subjects' discriminative performance in the test phase. In the remaining 10 trials of each test session, test stimuli were presented, so that each level of coherence (i.e. 60%, 50%, 40%, 30%, and 20%) was presented twice within the session. Apart from the constraint that in the first 4 trials training stimuli were presented, and that the side of presentation was balanced for each type of stimulus, the order and side of presentation of training and test stimuli were randomized within each session. Each dog could complete a maximum amount of 5 test sessions per day with an interval between sessions of at least 20 minutes.

Procedure for humans

The experiment was run in the same setting used for the dogs, with the exception that subjects sat on a stool at 150 cm from the monitors.

There was no preliminary training, but subjects received instructions on how to operate the keyboard, which they used to choose either the left or right monitor (by pressing left and right arrow keys, respectively). The sequence of the presentation was handled by the experimenter, who has been sitting behind the subject. In order to expose the human subjects to the stimuli for the same amount of time as it was for the dogs, subjects could not choose before at least 4 s were elapsed from the appearance of the stimuli on the monitor. Once a subject had performed a choice, a black screen appeared for 5 s before the next presentation. Human subjects underwent a training and a test phase similar to those described for dogs, with the only differences that in the training phase the learning criterion could be achieved within a single day and that in the test phase the maximum number of sessions that participants could complete within a single day was set at 10.

Ethical statement

The experiment involving dogs did not cause any pain, suffering or distress; for the experiment on humans, participation was voluntary, the experiment did not involve any risk or distress, and all the information regarding the aim and the procedure of the experiment were given beforehand, and informed consent was obtained from all human participants. No need of approval by local Ethics Committee was required by our institutions, in accordance with the current European and Italian legislation.

Data collection and statistical Analysis

Data about the choice performed by subjects in each trial were automatically collected with MATLAB (MATLAB version 7.10.0. Natick, Massachusetts: The MathWorks Inc., 2010) and, after the calculation of means. Data of each dog were fitted with a logistic function by using the routines provided by Palamedes (Pelli, 1997), which consider a proportion of correct response for the level of coherence given by as:

As the task was a 2-alternative forced-choice, the lower asymptote for guess (*Gamma*) was set to 0.5, while the upper asymptote (*Lambda*) was fixed by setting the lapse rate to 0.02. The parameters *Alpha* and *Beta* were left free. *Alpha* refers to the threshold, i.e. the value along the abscissa corresponding to the coherence level at which the function attains its steepest point. *Beta* is a discrimination parameter often referred to as the "slope".

An independents samples t-test was used to compare means of the *Alpha* and *Beta* parameters between our dogs and human participants

RESULTS

Dogs

The dogs needed between 33 and 85 sessions (median = 44) to reach the criterion of choosing the target stimulus (the one containing signal dots) with at least 90% of success in the training phase; all dogs maintained this success rate throughout the experiment.

Table 2.1 Values of the *Alpha* and *Beta* parameters and the estimated standard deviation for

 each of the five dogs

	Alpha	SD Alpha	Beta	SD Beta
Dog 1	37.6	3.7	0.095	0.04
Dog 2	37.4	5.8	0.048	0.01
Dog 3	40.5	4.4	0.068	0.02
Dog 4	41.8	3.9	0.086	0.03
Dog 5	53.9	3.5	0.104	0.07

Table 2.1 reports the *Alpha* and *Beta* parameters and their standard deviation for each dog. The mean threshold of coherent motion detection in dogs was at 42.2% of coherence. The mean value of the slope of the dog's psychometric function was 0.08.

Humans

All the participants reached the learning criterion within the minimum amount of six training sessions and they remained above this criterion for all the remaining training trials with 100% of success.

	Alpha	SD Alpha	Beta	SD Beta
Human 1	4.6	0.77	0.74	2.2
Human 2	4.7	0.66	0.73	2.3
Human 3	7.0	1.67	0.40	2.1
Human 4	4.6	0.73	0.61	1.5
Human 5	4.7	0.50	0.92	3.1

Table 2.2 Values of the *Alpha* and *Beta* parameters and the estimated standard deviation for

 each of the five humans

Table 2.2 reports the *Alpha* and *Beta* parameters and their standard deviation for each human participant. The mean threshold of coherent motion detection in humans was at 5.1% of coherence. The mean value of the slope of the human participant's psychometric function was 0.68.

Humans' *Alpha* was significantly higher (t = -12.08, P < 0.001) and humans' *Beta* significantly lower (t = -6.94, P = 0.002) than that of dogs.

DISCUSSION

In this study, we investigated coherent motion detection thresholds in domestic dogs, i.e. their ability to discriminate a signal stimulus with a variable proportion of dots moving in the same direction, from randomly moving dots display, with an accuracy of 75%. On average, dogs' threshold was equal to 42.2% coherence level of the signal stimulus. The threshold of human subjects tested in the same condition was significantly lower, with an average value of 5.1%.

This study included an initial training, which was successfully completed by all dogs within 80 training sessions, in line with other studies investigating various aspects of dogs visual processing (Pitteri et al., 2014; Kovacs et al., 2015) None of the dogs had difficulty in maintaining the set criterion in the training presentations of the test session. These findings support this procedure as a viable method for investigating motion processing in domestic dogs.

The range of thresholds found in our dogs spanned between 37% and 54%. Individual data shows that most of our subjects' thresholds fell in the 40% neighborhood, and only one subject's threshold seemed to deviate from this value. Nothing in the performance of the latter subject during training and test (e.g. speed of learning, ability to maintain criterion) or in its behavior, suggested explanations for its higher threshold not linked to motion processing, such as a lack in motivation, or learning difficulties. In addition, the overall variability shown by our dogs was proportionally lower than that of our human subjects, or that reported for other species, including pigeons (Bischof et al., 1999) and cats (Huxlin & Pasternak, 2004; Rudolph & Pasternak, 1996). Thus, we should retain this range as representative of a physiological individual variability in dogs' thresholds for coherent motion detection.

Dogs' threshold was considerably higher than that of our human participants. Of relevance, the consistent experimental condition soothed the impact on results of methodological differences; on the contrary, the latter hinder the possibility of a proper comparison with other studies. Factors such as the characteristics of stimuli, technologies to present stimuli and record data, and the type of populations involved (e.g. captive/experimental vs. companion animals), are source of substantial differences in thresholds for coherence motion detection. For instance, two independent studies report thresholds for cats between 5% and 9% in one case (Rudolph & Pasternak, 1996), and around 25% in the second case (Huxlin & Pasternak, 2004); a similar across-study variability is found in humans, with reported thresholds for healthy adult individuals ranging from 5% to 25% (Bischof et al., 1999; Rokszin et al., 2010). Even within the same study, modification of stimulus parameters, such as dot density, lifetime or speed, can dramatically influence detection thresholds in both humans and animals (Talcott et al., 2000; Weiffen et al., 2014; Rokszin et al., 2010). In this sense, the difference observed between our dogs and humans in the same experimental condition acquires particular significance, as it speaks against claims of a better, or even just a comparable ability of dogs in perceiving coherent motion with respect to humans.

What could be the source of such striking difference? From the neurobiological standpoint, the place to look at would be the cortical areas where the processing of motion is believed to occur; in humans, these processes are centered in the middle temporal area, and its up- and down-stream connections (Djavadian et al., 1983). There are sufficient differences between humans and dogs in the neuroanatomical structure of these neural pathways, to suggest that mechanisms and the limits of motion detection differ between these taxa (Aguirre et al., 2007; Jacobson et al., 1976) A previous study

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comparing humans and pigeons in the same tasks, reports values of humans' thresholds very similar to our human participants and pigeons' thresholds roughly similar to those of our dogs (Bischof et al., 1999). Pigeons' lower performance were attributed to a poorer integration of motion signals at both the local level, i.e. integrating the movement of a few dots across relatively long time intervals, and at the global level, i.e. integrating the paths of many dots across a large area of the display. Both mechanisms could have contributed towards the difference in detection of coherent motion by our dogs and humans. Our stimuli featured a relatively long dot lifetime (i.e. 1 s), allowing local motion integration to occur, and a high enough dot density to facilitate sampling of several dots at the same time, thus allowing global integration mechanisms. As such, we cannot speculate on which, if any, of these two mechanisms has more weight in explaining the differences between dogs and human, and further studies are needed to clarify this aspect.

One further aspect that could have contributed to the high threshold found in our dogs is experience with these types of/or with these specific stimuli. Although our dogs received 100 test presentations (20 per coherence level), in addition to a much higher number of training presentations, it is possible that their performance had not yet stabilized at the end of the testing phase. Effects of experience have indeed been documented, e.g. for mice (Douglas et al., 2006), monkeys (Chakraborty et al., 2015) and seals (Weiffen et al, 2014). In the latter, individual threshold decreased from 33.7% to 4.7% across the study. Although concurrent variations in other parameters do not allow a precise estimate of the effects of experience, these findings warrant verifying if our dogs' thresholds could be improved through further exposition to the experimental stimuli.

Regardless of the underlying mechanisms, comparative aspects of motion detection

could also be looked at from an ecological perspective. In this sense, feeding strategies not relying on detecting movement, such as scavenging, predominate in the ecological niche occupied by the so-called village dogs, which are believed to provide a good example of dogs in earlier stages of domestication (Gacsi et al., 2009). Thus, canine domestication may have relaxed pressure on the need for a visual system highly specialized in motion detection.

In conclusion, this study indicates that the threshold for the detection of coherent motion is higher in dogs than it is in humans. What precise mechanisms underlie these differences is still to be investigated. Possible factors include experience, and the relative role of local and global motion processing, which are currently being addressed by our research group.

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CHAPTER 3

The effects of Dot Density, Dot Lifetime and Perceptual Learning on Coherent Motion Detection Thresholds in Dogs (Canis Familiaris)

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INTRODUCTION

Being able to identify preys, and predators can make a difference in the survival ratio of the individual, thus the ability of detecting motion is one of the primal features of the visual system that started to emerge early in evolution (Ghering, 2012). Perceiving coherent motion is provided by the visual system through detecting units of local motion signals and integrating them over space and time (Braddick, 1993; Williams and Brannan, 1994). This phenomenon is commonly investigated by discrimination tasks of random-dot displays (Newsome and Pare, 1988), where a visual pattern of a given number of motion units (e.g. dots) are coherently moving in the same direction (signal), among dots moving in random directions (noise). The smaller the proportion of signal dots, that are needed to allow the subject to perceive coherent motion, the lower is the individual threshold of detecting coherent motion.

Through domestication and facing challenges while adapting to the human environment, dogs earned to become one of the most promising model species to investigate human cognition from a comparative and evolutionary aspects (Miklosi et al., 2004). In the last decades several studies have investigated dogs' abilities of using visual cues in social situations and reported that dogs have a special ability to use such visual information in communicating with human partners, involving pointing, gazing, bowing (Hare and Tomasello, 1999; Soproni et al., 2001), as well as recognizing complex and subtle human facial expressions and interpreting them as visual cues (Buttelman and Tomasello, 2013). Beside the majority of studies on socio-cognitive mechanisms underlying dogs' ability to recognize, interpret and use visual cues, only a handful of behavioral studies have investigated fundamental functions of dogs' visual system and have revealed that dogs are able to discriminate global and local features of static visual stimuli (Pitteri et al., 2014) and they have the ability to discriminate biological- from non-biological motion (Kovacs et al., 2016).

In our recent study we found the threshold for coherent motion detection at 42% of coherence in dogs which is much higher than the 5% of coherence that we found in human subjects assessed by the same test (Kanizsar et al., 2017) and of what is reported in phylogenetically closer species such as monkeys (Newsome and Pare, 1988) seals (Weiffen et al., 2014) and cats (Rudolph and Pasternak, 1996; Huxlin and Pasternak, 2004). Our findings are similar to what is reported by Bischof and collegues (1999) who investigated motion detection thresholds in humans and pigeons and attributed the higher thresholds of pigeons to their poorer ability in integrating local motion units due to either the decreased lifetime or density of the dots. However, these parameters of the stimuli were stable across our previous study and the systematic manipulation of them is needed to clarify their possible effect on dogs' perception. Since the sensation of coherent motion is a result of the integration of local motion units (Braddick, 1974; 1993) it is evident that the more energy (e.g. density and lifetime) a visual stimulus have, the more source of information the visual system can integrate, the earlier it is able to detect coherent motion. Accordingly, the number of local motion units (dot density) and the time each unit's path is visible (dot lifetime) are crucial parameters of the visual stimulus and it has been proved that manipulating these parameters can notably effect coherent motion detection thresholds in both human and non-human subjects (Talcott et al., 2000; Snowden and Kanavagh, 2006; Weiffen et al., 2014).

Another factor that is possibly modifying individuals' performance in visual discrimination tasks is the effect of perceptual learning. This cognitive mechanism is an experience-dependent perceptual improvement, enabled by the plasticity of the visual system (Zohary et al., 1994; Gilbert, 1996). It consists in the ability of rapid adaptation

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to the continuously changing environment and triggered by frequent encounters with certain visual stimuli (Karni and Sagi, 1993; Watanabe et al., 2001). In the last decades this phenomenon has been widely investigated in adult humans over various visual tasks and reported to improve the performance of the subjects in texture (Karni and Sagi, 1991) and motion discrimination (Liu and Vaina, 1998) as well as coherent motion detection in humans, mice, monkeys and seals (Britten et al., 1992; Watanabe et al., 2001; Douglas et al., 2006; Weiffen, 2014). However, it has not yet been investigated whether perceptual learning is present in dogs.

Continuing the research line of our previous study, in these current experiments we aimed to investigate the possible mechanism, underlying the notable difference between dogs, humans and other species regarding to coherent motion detection thresholds. The stimuli of our previous study were created accordingly to what is known about the perception of coherent motion in other species (Newman and Pare, 1988; Bischoff et al., 1999; Huxlin and Pasternak, 2004; Weiffen, 2014). With its relatively high dot density (8.7 dots/deg^2) and dot lifetime (1 sec), the stimuli served as a proper base for going further in understanding whether manipulation of stimulus features (e.g. decreased dot density and decreased dot lifetime) can affect dogs' performance and if the repeated encounter with the stimuli could trigger the cognitive mechanisms of perceptual learning. This latter phenomenon would result in an improved perception of the stimulus coherent motion, thus would lower the primarily assessed individual thresholds. For this aim we used random dot displays for a two-way conditioned discrimination task in which we systematically manipulated the dot density (Dot Density Test), dot lifetime (Dot Lifetime Test) and we re-assessed the subjects' thresholds after extensive exposure to the stimuli (Perceptual Learning Test).

MATERIALS AND METHODS

Subjects

We had five (mesocephalic) pet dogs, three females (1 Golden Retriever, 1 Mudi, 1 Siberian Husky) and two males (1 Cocker Spaniel, 1 Labrador-Poodle Mix 'Labradoodle'), between 3 and 11 years of age in our sample. All of these dogs had participated in the previous study that investigated thresholds of coherent motion detection in dogs and humans (Kanizsar et al., 2017). All the dogs belonged to private owners who were workers and students of the University of Padova and participated in the experiments on a voluntary basis. The subjects underwent a veterinary examination before the enrollment in the experiments to exclude health conditions that would prevent them from participation. Dogs were selected upon the requirement that they were highly motivated for food and willing to cooperate, while feel comfortable with being in the laboratory.

Ethical statement

The experiment involving dogs did not cause any pain, suffering or distress for the participants. Thus, no need of approval by local Ethics Committee was required by our institutions, in accordance with the current European and Italian legislation.

Stimuli

All experimental stimuli were created with MATLAB (MATLAB version 7.10.0. Natick, Massachusetts: The MathWorks Inc., 2010), using features of Psycho Toolbox (Brainard, 1997; Pelli, 1997). The stimuli were displayed on a black area of 31.1 cm x 31.1 cm (24.0 x 24.0 deg, from the viewing distance of 70 cm), where white dots with a diameter of 0.16 cm moved at a speed of 19.4 cm/s (15.0 deg/s). In all trials of the training and experimental phases, the noise stimulus had a coherence level of 0%, that is all of the dots moved in random directions. For all the training trials (including those integrated in the set of stimuli for the experiments) the signal stimulus was set at a coherence of 80%, i.e. 80% of the dots moved in the same direction (towards the left side of the display), whereas the remaining 20% moved in random directions. Detailed description of the test stimuli of each experimental phases are given below.

Experimental setting

All the experiments took place in the Laboratory of Applied Ethology of the Department of Biomedicine and Food Science (University of Padova, Italy). A testing area of 2.5 x 3 m has been established in a laboratory room. Stimuli were presented on two monitors (VG248QE, ASUSTeK Computer Inc., Taipei, Taiwan), that were identical with a refresh rate set at 120 Hz; this parameter of the setting was meant to prevent possible biases on dogs' detection of motion, due to their higher flicker fusion frequency (Miller and Murphy, 1995). Monitors were connected to a PC (Optiplex 960, Dell Inc., Round Rock, Texas, USA) and were placed 25 cm away from each other, on two height-adjustable stands, thus their height have been set at eye level for each subject. Presentations were controlled by the experimenter with a Bluetooth keyboard (Logitech).

Procedure

All subjects completed a shaping and training phase as part of a previous study (Kanizsar et al., 2017). These phases were meant to familiarize dogs with the usage of the equipment and to reach a strict criterion of being able consistently discriminate the training signal stimulus as a base of being enrolled in further experiments. The training phase was repeated before each tests in order to re-assure the maintenance of the criterion of choosing the signal stimulus with 90% accuracy (at least 18 correct choices out of 20 trials in 6 consecutive sessions).

Assessment of coherent motion detection thresholds (Assessment Test)

Prior to the present study, subjects undergone an assessment test which meant to define each dog's threshold of detection of coherent motion. Details of the procedure and the set of stimuli used in this phase is described in our previous study (Kanizsar et al., 2017). Thus, the stimuli featured the parameters of 8.7 dots/deg² dot density and 1 sec dot lifetime and 15 deg/sec dot speed. The Assessment Test consisted of 10 sessions each composed by 24 trials. In the first 4 trials of each session, dogs were presented with the training signal stimuli (80% coherence), as a 'warm-up' and 10 additional training trials were randomly distributed among the test trials within each sessions to maintain dogs' motivation and control of subjects' discriminative performance in the test phase. Among the rest of the trials of each test session, test stimuli were presented with different levels of coherence (i.e. 60%, 50%, 40%, 30%, and 20%) each have been shown twice within the session. The order and side of presentation of training and test signal stimuli were randomized within each session, except for the fixed 4 warm-up initial trials.

Effect of Dot Density (Dot Density Test)

This phase was meant to investigate whether the manipulation of the density of the presented dots could affect individual thresholds of coherent motion detection. The presented stimuli were the same throughout the 10 test sessions: contained 4 warm-up initial trials with the training stimulus, followed by 6 test trials with stimuli with 3 different levels of dot density (8.7 dots/deg², 2.3 dots/deg² and 0.23 dots/deg²) that were randomly distributed among 10 training trials. Every level of dot density were shown twice per session. Dot lifetime had the same value as for the training signal stimulus (1 sec) while the coherence levels were set to the individual threshold value, which was identified in the previous Assessment Test, for each subject.

Effect of Dot Lifetime (Dot Lifetime Test)

This phase was meant to investigate whether the manipulation of the lifetime of the dots could affect the individual thresholds of the subjects. The 10 sessions were composed of 20 trials: 4 warm-up initial trials with the training stimulus, 6 test trials where signal stimuli had manipulated dot lifetime on three different levels (0.99 sec, 0.5 sec and 0.02 sec) randomly distributed among further 10 training trials. In this test, the density of dots was the same as for the training stimulus (8.7 dots/deg²) while the level of coherence was set to the individual threshold value of each subject, that was identified as a result of the Assessment Test.

Effect of Perceptual Learning (Perceptual Learning Test)

In this final phase of the experiment, the procedure of the Assessment Test was repeated with identical stimuli that were used in the previous Assessment Test to investigate whether Perceptual Learning Effect occurred through being exposed to the signal stimuli for 640 trials. The average time that elapsed between the last day of the Assessment test and the first day of the Perceptual Learning Test were 2 months.

Data collection and statistical Analysis

In the Assessment and Perceptual Learning Test, data of each dog were fitted with a logistic function by using the routines provided by Palamedes (Prins and Kingdom, 2009), which consider a proportion of correct response for the level of coherence given by as:

$$P(C; \alpha, \beta, \gamma, \lambda) = \gamma + \frac{1 - \gamma - \lambda}{1 + e^{-\beta(C - \alpha)}}$$

As the task was a 2-alternative forced-choice, the lower asymptote for guess (*Gamma*) was set to 0.5. The upper asymptote (*Lambda*) and the parameters *Alpha* and *Beta* were left free. *Alpha* refers to the threshold, i.e. the value along the abscissa corresponding to the coherence level at which the function attains its steepest point. *Beta* is a discrimination parameter often referred to as the "slope". Then, a one-tail paired t-test was run for threshold, slope and upper asymptote, regardless the small sample size, in order to investigate whether the parameters of the Assessment Test and the Perceptual Learning Test differ.

Different regression analyses were run to find the best models for describing the relationships between the dots density and the proportion of correct response in Dot Density Test and between dots lifetimes and the proportion of correct choice in Dot Lifetime Test. After that, a one-tail one sample t-test was run to determine whether the mean slope of the functions was significantly different from zero, indicating better (> 0) or worse (< 0) performance (when the independent variable increases).

RESULTS

Effect of Dot Density

Figure 1 shows the proportion of correct choices as a function of dot density $(dots/deg^2)$. An optimum way to fit these data is a simple linear model (see table 1 for individual slopes, intercepts and the R²). Indeed, dog's performance improves as the number of dots within a deg² increases. A one-tailed one-sample t-test showed that the slope of the linear regression was significantly higher than zero ($t_{(4)}$ = 3.58, P= 0.011, Cohen's d = 2.58).

Figure 3.1



Figure 3.1 Dot Density Test. Proportion of correct choices performed by each dogs when test signal stimuli had 3 different levels of dot density. Symbols are indicating the proportion of correct choices while lines represent the linear regression of the data of each subject.

Table 3.1 Dot Density Test. Values of *slope, intercept* and R^2 of the linear regression of the data of each of the five dogs.

	Slope	intercept	R^2
Dog 1	0.035	0.54	0.91
Dog 2	0.005	0.69	0.97
Dog 3	0.017	0.57	0.91
Dog 4	0.014	0.53	0.81
Dog 5	0.017	0.56	0.83

Effect of Dot Lifetime

Figure 2 shows the proportion of individual correct choices as a function of dot lifetimes (second). Data showed that dog's performance increases rapidly as the dot lifetime increases but then it stabilizes. Therefore, a simple linear model is not optimal in this condition. The best model was fitting the data with a logarithmic function. Indeed, the R² of four out of five dog is higher than 0.7 (see table 3). Furthermore, a one-tail one-sample t-test showed that the slope of the logarithmic regression was significantly higher than zero ($t_{(4)} = 4.68$, P= 0.004, Cohen's d = 3.3).





Figure 3.2 Dot Lifetime Test. Proportion of correct choices performed by each dogs when test signal stimuli had 3 different levels of dot lifetime. Symbols are indicating the proportion of correct choices while lines represent the linear regression of the data of each subject.

	Slope	intercept	R^2	
Dog 1	0.14	0.91	0.75	
Dog 2	0.08	0.76	0.97	
Dog 3	0.09	0.88	0.84	
Dog 4	0.06	0.81	0.71	
Dog 5	0.03	0.66	0.28	

Table 3.2 Dot Lifetime Test. Values of *slope, intercept* and R^2 of the linear regression of the data of for each of the five dogs.

Effect of Perceptual learning

Figure 3 shows the dog's psychometric functions of the Assessment Test, the Perceptual Learning Test and the proportion of correct choices for each level of coherence, whereas Table 3 shows the *Alpha* and *Beta* parameters and their standard deviation for each dog. The mean threshold of global motion detection in dogs in the Assessment Test was at 42.2% of coherence whereas in the Perceptual Learning Test it was 29.8%. The mean value of the slope in the Assessment Test was 0.067, and in the Perceptual Learning Test was 0.056. A one-tail paired t-test was run for threshold, slope and upper asymptote, regardless the small sample size. The difference in threshold approaches significance ($t_{(4)}=1.96$, P = 0.06, Cohen's d = 1.28) as well as the difference in slope ($t_{(4)}=1.63$, P = 0.09, Cohen's d = 0.57). The upper asymptote was similar before and after the training ($t_{(4)}=1.12$, P = 0.14, Cohen's d = 0.38).

Figure 3.3



Figure 3.3 Dog's psychometric functions in the Assessment Test (dotted line), in the Perceptual Learning Test (black line) and the proportion of correct choices (Assessment Test: empty circle; Perceptual Learning Test: filled black circle) for each level of coherence.

Table 3.3 Values of the *Alpha* and *Beta* parameters and the estimated standard deviation for each of the five dogs in the Assessment Test (AT) and Perceptual Learning Test (PL)

1		Ĩ	
37.93	0.09	33.9	0.06
32.53	0.06	38.54	0.05
40.62	0.07	26.07	0.07
41.83	0.08	30.33	0.07
37.71	0.04	19.96	0.04
	37.93 32.53 40.62 41.83 37.71	37.93 0.09 32.53 0.06 40.62 0.07 41.83 0.08 37.71 0.04	37.93 0.09 33.9 32.53 0.06 38.54 40.62 0.07 26.07 41.83 0.08 30.33 37.71 0.04 19.96

Alpha AT Beta AT Alpha PLT Beta PLT

DISCUSSION

In this study we have investigated whether the recently found 42% of coherence threshold of detecting coherent motion in dogs (Kanizsar et al., 2017) can be influenced by sensitivity to the dot density and the dot lifetime of the presented stimuli and by the subjects' repeated encounter with the signal stimulus. Our results show that both density and lifetime of the dots took an impact on the performance of the subjects and, thus it is decreased with lowered dot density and dot lifetime. This is in line with what was found in other species, such as in pigeons and humans where Bischof and

colleagues (1999) found that the percentage of correct choices increased with longer dot lifetime in both species, and with the results of Weiffen and coauthors (2014) who reported that both increasing dot lifetime and dot density of the stimuli can positively affect seals performance in random dot display tasks. As we mentioned in the introduction of this study, perceiving coherent motion starts with the recognition, and integration of local motion units (e.g. moving dots). Visual patterns that consist several motion units is also occupying a greater proportion of space and time in the visual field, providing more information for the visual system, which serves the ability of perceiving coherent motion. Thus, the less information the organism is provided with, the more difficult it is to perceive and integrate local motion units resulting in a higher threshold of detecting coherent motion.

Moreover, our data showed that the repeated and extensive encounter with the signal stimuli lowered coherent motion detection thresholds of the dogs to from 42% to 30% of coherence. Even though the effect size tends to be larger than the true population effect in studies with a small sample (Brand et al., 2008), four out of five dogs showed a clear perceptual improvement, which allow us to cautiously conclude, that perceptual learning has been triggered in the subjects and could affect the performance of the dogs. The presence of perceptual learning is also supported by the fact that perceptual learning forms slowly - as a result of implicit recognition of patterns through repeated experience - then escalates rapidly before consolidating on a plateau, drawing an S-shaped, sigmoid learning curve (Stickgold et al., 2000; Nemeth et al., 2009). This typical pattern is the same we observed in the initial training (that has been conducted before the Assessment Test in our previous study), where dogs showed a relatively long (50-80 sessions) period of reaching the learning criterion of discriminating the signal stimulus (80% coherence) from the negative stimulus (0% coherence). However once,

they reached it, none of them have fallen below the criterion during the following experiments nor in the re-training sessions between them. Visual perceptual learning considered to be the primal form of implicit learning (Watanabe et al., 2001), that is sensitive to the low level features of the training stimulus. In a visual discrimination task, experience-dependent perceptual improvement occurs only in tests conducted with stimuli that have the same features (e.g. horizontal motion) as the training stimuli and for seeing improvement in discrimination tasks with stimuli with different parameters (e.g. vertical motion) subjects need to be trained and re-trained (Kozma et al., 2005). This suggests cortical origins of perceptual learning, since motion direction selectivity appears first in the V1 visual cortex (Fiorentini and Berardi, 1980). Moreover, according to the results of Stickgold and coauthors (2000) visual perceptual learning is also sensitive for spatial frequency (e.g. dot density and dot lifetime) together with the already mentioned direction of motion.

Considering these, the presence of perceptual learning in dogs is supported by the relatively long period of learning to discriminate the initial training stimulus and then maintaining it with 90% accuracy throughout the following experiments. Perceptual learning is also reported to build as a time consistent, solid skill that can be retained for years (Karni and Sagi, 1993) and some of the preliminary data of our studies that are currently in progress seems to support these findings. Namely, 'expert dogs', that participated in our previous and present studies, are reaching the learning criterion of discriminating visual stimuli at least three times faster than dogs that are freshly enrolled and naive to the task.

As we mentioned in the introduction, experience related improvement in coherent motion detection have been investigated already in humans (Watanabe et al., 2001), mice (Douglas et al., 2006) and monkeys (Britten et al., 1992), yet it has not been reported to occur in dogs according to the best of our knowledge.

Even though the present study brought us further in understanding motion perception in dogs, it is still not clear if their higher threshold in detecting coherent motion is due to their limitations in visual perception or due to methodological biases.

As a conclusion we can cautiously say that according to the results of this study, perceptual learning is present in dogs and their higher thresholds of coherent motion detection, compared to other species can be decrease by experience. This plasticity of visual perception is also supported by our results of dogs' sensitivity to changes for lower level parameters of visual patterns. These findings are facilitating a deeper understanding on the cognitive mechanism of motion perception and visual learning in dogs as well as rising new research questions that are currently being investigated by our research group.

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CHAPTER 4

Movement detection thresholds in dogs (Canis familiaris)

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INTRODUCTION

Detection of movement is considered as one of the major factors that can trigger and influence motion perception. Being able to discriminate stationary visual patterns from moving ones is crucial for adaptive behavior as well as for increasing the survival ratio of both humans and animals.

Perception of visual movement have been studied in humans starting from 1960's (Gibson, 1968; Graham, 1968), however this specific aspect of visual perception has not yet been widely investigated in animals except for the early review of Kennedy (1936) and a study by Hodos and coauthors (1976) that studied threshold of velocity in pigeons. In their study, they reported that the lowest speed at which pigeons are able to discriminate a stationary from a moving visual stimulus varied between 4.1 and 6.1 deg/s (Hodos et al., 1976). Conversely, a more recent study that compared speed thresholds in human adults and 5 years old children found that adults need at least 0.4 deg/s velocity difference between two visual stimuli to be able to discriminate them, while 5 years old children showed a higher threshold of 1.1 deg/s which suggests that the system, underlying the mechanisms of this specific aspect of motion perception might be immature at the age of 5 years (Ahmed et al., 2006). Additional studies (Ellemberg et al., 2004; Aslin and Shea, 1990) are supporting this theory thus reporting velocity thresholds to be at approximately 9 deg/s in 6 weeks old infants that is dropping to 4 deg/s at the age of 12 weeks.

Previous studies of this PhD project aimed to first define thresholds of coherent motion perception in dogs, then refine the findings by going deeper in investigating which features of the stimuli could influence the performance of the participants. In the study of Chapter 2, we found that the threshold for detecting coherent motion in dogs is higher compared to what is found in other species, such as in human adults, infants and pigeons, (that were tested in similar experimental conditions; Kanizsar et al., 2017). The second and third studies of Chapter 3, revealed that specific parameters of the stimuli can affect dogs' performance, thus decreased dot density and dot lifetime is resulting in decreased performance, however repeated encounters and gaining experience with the stimulus may trigger the mechanisms of perceptual learning in dogs.

However there is still no data in the literature on whether and at which threshold dogs are able to discriminate stationary and moving visual patterns. Aiming for a better and more complex understanding of the mechanisms that underlines dogs' visual cognition and deepening our knowledge on the characteristics of motion perception, in this current study we investigated thresholds of movement detection in pet dogs, thus measuring the lowest speed (movement detection threshold) of coherent motion that can be discriminated from a stationary stimulus by the subjects. Considering the data of previous studies, reviewed above, together with the results of the studies of previous chapters of this PhD thesis, we might suspect that speed detection thresholds in dogs could be higher than that is reported in human adults, lower than what is reported in 6-month-olds and 12-month-olds children, while similarly to the results of other comparative studies on cognitive skills of human infants and pet dogs (Tomasello & Kaminsky, 2009; Topal et al., 2009) dogs' threshold should be most similar to what is reported in 5 years old children.

For this aim we used discrimination tasks in which dogs had to choose a static image of dots (speed = 0 deg/s, reference stimulus RS) against a moving stimulus with the same characteristics (moving stimulus, MS).

METHODS

Subjects

Our sample is composed of 4 pet dogs by far, three females and one male, between 2 and 11 years age of the following breeds: Cocker Spaniel, Whippet, and 2 mixed breeds.

The owners were all workers of the University of Padova and participated in the experiments on a voluntary basis. None of the enrolled subjects have any health conditions that would prevent them from participation. Dogs were selected on the criterion of being highly motivated for food and the be willing to cooperate while feeling comfortable with in the laboratory.

Stimuli

Stimuli were created with MATLAB (MATLAB version 7.10.0. Natick, Massachusetts: The MathWorks Inc., 2010), using features of Psycho Toolbox^{32,33}. The stimuli were shown on a black squared area of $31.1 \times 31.1 \text{ cm}$ (24.0 x 24.0 deg, from the viewing distance of 70 cm). We used two types of stimuli both during the training and experimental phases. A referential stimulus (RS) of a static image, presenting 5000

white dots (8.7 dots/deg² density) with a diameter of 0.16 cm, and a moving stimuli (MS) with the same parameters regarding to dot size and density, with a constant dot lifetime (1 sec) and coherence level (80% of the dots moved coherently in the same direction, whereas 20% of the dots moved randomly). During the training phase, the dots of MS moved with a velocity of 15 deg/s while in the test phase the speed of the stimuli was manipulated and varied between 15 deg/s and 0.12 deg/s.

Dot size, density and coherence level were chosen based on stimuli that were previously used for testing other species in similar experiments^{8,34} and on our results of previous studies, investigating coherent motion detection threshold in dogs (Kanizsar et al., 2017) and the effects of dot density and lifetime on coherent motion detection in dogs (Kanizsar et al., *under preparation*).

Experimental setting

All the experiments took place in the Laboratory of Applied Ethology of the Department of Biomedicine and Food Science (University of Padova), in a testing area of 2.5 x 3 m. Stimuli were presented on two identical monitors (VG248QE, ASUSTeK Computer Inc., Taipei, Taiwan), whose refresh rate was set at 120 Hz due to dogs' higher flicker fusion frequency²¹. Monitors had touch-screen capabilities, so touches of their surface (i.e. choices of either stimulus, as detailed below) were automatically recorded. Monitors were connected to a PC (Optiplex 960, Dell Inc., Round Rock, Texas, USA). Monitors were placed 25 cm away from each other, on two height-adjustable stands, so their height could be set at eye level for each subject. Presentations were controlled with a Bluetooth keyboard (Logitech).

Training phase

Initially, 2 out of 4 dogs underwent a preliminary phase, in which they were shaped to touch the screen with the nose and got accustomed to the trial procedure. The protocol was identical to what was carried out in our first study (see Chapter 2 for detailed description of this phase) and in which 2 of the 4 subjects have already participated in. This phase was aimed at training all dogs to discriminate the static reference stimulus (RS) from the moving stimulus (MS). Dogs underwent sessions of 20 consecutive trials, in which the RS (0 deg/s) and the MS (15 deg/s) were presented. The side of presentation of the two stimuli was randomly chosen by the software and balanced within the 20 trials. Each dog underwent a maximum of 5 training sessions per day, with an interval between session of at least 20 minutes. Dogs were only fed at the end of the day, in the days in which they were involved in the study. Subjects could proceed to the subsequent test phase when they chose the RS for at least 18 out of 20 trials (i.e. 90% accuracy) in 6 consecutive sessions, distributed over two separate days.

Test phase

This phase was meant to assess dogs' velocity threshold for perception of coherent motion. Sessions of this phase were composed of maximum 30 trials with alternations of 3 trials with the 'Training Trial' (TR) and 3 trials of 'Test Trial' (TT). The speed of referential stimuli (RS) was 0 deg/s in all Training and Test Trials, whereas the speed of moving stimuli (MS) varied accordingly the performance of each individual (details are discussed below at each Assessment tests). The side of RS and MS presentation were randomized within the sessions. Each dog could complete a maximum amount of 5 test sessions per day with an interval between sessions of at least 15 minutes. Subjects
participated in four Assessment tests in the following order:

- 1) Descending Assessment 1
- 2) Ascending Assessment 1
- 3) Descending Assessment 2
- 4) Ascending Assessment 2.

For the Descending Assessments, each time the dogs committed none or maximum one error in the batch of three Test Trials, the speed of the MS in the subsequent batch of Test Trials were halved. If the dog committed two or more errors, the speed of the subsequent batch of Test Trials remained the same as the previous ones. In case a dog committed two or more mistake at a particular speed in three consecutive batches of Test Trials the assessment was terminated. For the Descending Assessment 1 the initial speed of the moving stimuli (MS) of the Test Trials (TT) were set to 7.5 deg/s. If the dog succeeded on all levels of a session, or committed two or more mistakes only in the last two batches of Test Trials, the experimenter saved the last value of speed that was administered and started the following session with that value as the initial speed of the MS of the TT. The speed value at which the subject failed to complete a successful batch three times in a row was assessed as the Descending Threshold 1 (DT1). For the Descending assessment 2 the same procedure was carried out as described above, except for that the initial speed of the moving stimuli (MS) of the TT - regardless of the speed value of DT1 – were set to 4,5 deg/s. After every batch of TT in which the dog committed none or maximum one mistake, the speed value was halved for the next batch of TT and the value at which the subjects failed for 3 consecutive batches of TT was assessed as Descending Threshold 2 (DT2).

For the Ascending Assessment, each time the dog committed two or more mistakes within a batch of three test trials (TT), the speed of the moving stimuli of the subsequent batch of TT was doubled. If the dog committed one or no mistake, the speed of the subsequent batch of TT remained the same as the previous one. When a dog succeeded at a particular speed for three batches the assessment was terminated. For the Ascending Assessment 1 the initial speed of the moving stimuli (MS) of the Test Trials were set to the individual DT1/1.5 deg/s for each subject. If the dog failed on all levels of a session, or succeeded only in the last two batches of Test Trials, the experimenter saved the last value of speed that was administered and started the following session with that value as the initial speed of the MS of the TT. The speed value at which the subject succeeded to complete a successful batch three times in a row was assessed as the Aescending Threshold 1 (AT1). For the Aescending Assessment 2 the same procedure was carried out as described above, except for that the initial speed of the moving stimuli (MS) of the test TT were set to the individual value of DT2/1.5 deg/s for each subject, regardless of the speed value of DT1. After every batch of TT in which the dog failed, the speed value of the MS was doubled for the next batch of TT and the value at which the subjects succeeded for 3 consecutive batches of TT was assessed as the Ascending Threshold 2 (AT2).

DATA COLLECTION AND PRELIMINARY RESULTS

Data about the choice performed by subjects in each trial were automatically collected with MATLAB (MATLAB version 7.10.0. Natick, Massachusetts: The MathWorks Inc., 2010) and, after the assessment of the two values of descending thresholds (DT1 and DT2) and two values of ascending thresholds (AT1 and AT2), the calculated means

gave the individual levels of velocity thresholds of the subjects (see **Table 4.1**) Our preliminary results show that the velocity thresholds for dogs varying between 0.45 and 1.5 deg/s with a mean value of 0.9 deg/s.

	Speed (deg/s)				
Dog ID	DT1	AT1	DT2	AT2	тн
Dog 1	0.117	0.312	0.564	0.750	0.45
Dog 2	0.117	0.312	0.564	0.375	0.36
Dog 3	0.939	1.248	1.125	1.500	1.23
Dog 4	0.939	1.248	0.564	1.500	1.50

Table 4.1 This table shows the lowest speed of the stimuli at which, each subject was able to discriminate the moving stimulus from the stationary one during the Descending Assessment 1 and 2 (DT1 and DT2), Ascending Assessment 1 and 2 (AT1 and AT2) and the velocity thresholds (TH) calculated based on the means of DTs and ATs.

DISCUSSION

According to our preliminary results the mean threshold of detecting coherent motion velocity in our dogs is at the speed of 0.9 deg/s. This performance is higher than what is reported in adult humans, who need a 0.4 deg/s difference between two stimuli to be able to discriminate speed and lower than what is reported in 5 years old children who

need a speed difference of 1.1 deg/s (Ahmed et al., 2005). However, dogs' results are still showing more similarity to what is found in humans compared to the thresholds reported in pigeons that is between 4 and 6 deg/s (Hodos et al., 1976).

It also need to be noted that among the four subjects that participated in this study, two dogs - Dog 3 and Dog 4 - have already participated in the previous studies of this PhD project, while other two of them - Dog 1 and Dog 2 - were naive to the procedure before being enrolled in this study. According to our findings, reported in Chapter 3, repeated encounters with certain visual patterns may trigger the mechanisms of perceptual learning that may result in lower thresholds of detecting coherent motion. However, we found thresholds of movement detection to be lower and very similar in the two naive dogs. Here it should be highlighted that results of several studies (Churchland & Lisberger, 2001; Liu & Newsome, 2003) suggests that the mechanisms, providing the ability of the calculation of speed are more complex than the ones coding direction, coherence, density and other features of a visual pattern that have been studied also through the experiments of this PhD project and in which the 'experienced' dogs - Dog 3 and Dog 4 - have participated before completing the current tests. Accordingly, previous experience with the stimuli might not enhanced the performance of the subjects in discriminating the moving stimulus (MS) from the reference stimulus (RS). In contrary, as a result of interference in their memory of MS as the 'positive stimulus' their choices might have been biased toward choosing MS, in spite of it served as the 'negative stimulus' in this experiment. This means that in the training phase of this study, Dog 3 and Dog 4 underwent 'reversal training' while Dog 1 and Dog 2 learned to discriminate MS and RS as a first encounter with the stimulus.

Even though these are preliminary results - which makes drawing conclusions problematic - we must note that, the results of the two 'naive dogs' (Dog 1 and Dog 2) might show more clear data than 'experienced dogs' (Dog 3 and Dog 4) who went through reversal learning. Interestingly, the 'naive dogs' of this study show very similar thresholds (0.4 deg/s) of detecting movement to what is reported in human adults (0.4 deg/s) by Ahmed and colleagues (2005), however additional data is required to be collected to draw a conclusive picture of dog's ability to perceive motion.

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CHAPTER 5

General discussion

In PhD project, we first investigated coherent motion detection thresholds in domestic dogs, i.e. their ability to discriminate a signal stimulus with a variable proportion of dots moving in the same direction, from randomly moving dots display, with an accuracy of 75%. On average, dogs' threshold was equal to 42.2% coherence level of the signal stimulus. The threshold of human subjects tested in the same condition was significantly lower, with an average value of 5.1%.

Here we must note that our stimuli in this first study featured a relatively long dot lifetime (i.e. 1 s), allowing local motion integration to occur, and a high enough dot density to facilitate sampling of several dots at the same time. As such, we could not speculate on which, if any, of these two mechanisms has more weight in explaining the differences between dogs and human, and further studies were needed to clarify this aspect.

In addition, another aspect could have affected the high threshold found in our dogs that is experience with these specific type of visual pattern. Our results in the second study revealed that both the density of dots and lifetime of the dots took an impact on the performance of the subjects and, thus it is decreased with lowered dot density and dot lifetime. This is in line with what is found in other species, such as in pigeons and humans where Bishof and collaborators (1999) found that the percentage of correct choices increased with longer dot lifetime in both species, and with the results of Weiffen and coauthors (2014) who reported that both increasing dot lifetime and dot density of the stimuli can positively affect seals performance in random dot display tasks. As we mentioned in the introduction, perceiving coherent motion starts with the recognition, and integration of local motion units (e.g. moving dots). Visual patterns that consist several motion units is also occupying a greater proportion of space time in the visual field, providing more information for the visual system, which serves the ability of perceiving coherent motion. Thus, the less information the organism is provided with, the more difficult it is to perceive and integrate local motion units resulting in a higher threshold of detecting coherent motion. Moreover, we also found that the repeated and extensive encounter with the signal stimuli lowered coherent motion detection thresholds of the dogs to from 42% to 30% of coherence. Even though the effect size tends to be larger than the true population effect in studies with a small sample (Brand et al., 2008), four out of five dogs showed a clear and relevant perceptual improvement, which allow us to cautiously conclude, that perceptual learning has been triggered in the subjects and could affect the performance of the dogs. Our further study that assessed motion velocity thresholds in dogs revealed according to preliminary results - that the mean threshold of detecting coherent motion velocity in our dogs is at the speed of 0.9 deg/s. This performance is higher than what is reported in adult humans, who need a 0.4 deg/s difference between two stimuli to be able to discriminate speed and lower than what is reported in 5 years old children who

need a speed difference of 1.1 deg/s (Ahmed et al., 2005). However, dogs' results are still showing more similarity to what is found in humans compared to the thresholds reported in pigeons that is between 4 and 6 deg/s (Hodos et al., 1976).

In conclusion, the studies of this PhD project indicate that the threshold for the detecting coherent motion is higher in dogs than it is in humans. The exact mechanisms underlie these differences are still need further investigations, however results suggest that possible factors are certain features of the visual pattern (e.g. density, lifetime, speed) as well as experience and the role of perceptual learning.

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