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Visual event-related potentials of dogs: a non-invasive electroencephalography study

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Abstract Previously, social and cognitive abilities of dogs have been studied within behavioral experiments, but the neural processing underlying the cognitive events remains to be clarified. Here, we employed completely non-invasive scalp-electroencephalography in studying the neural correlates of the visual cognition of dogs. We measured visual event-related potentials (ERPs) of eight dogs while they observed images of dog and human faces presented on a computer screen. The dogs were trained to lie still with positive operant conditioning, and they were neither mechanically restrained nor sedated during the measurements. The ERPs corresponding to early visual processing of dogs were detectable at 75–100 ms from the stimulus onset in individual dogs, and the group-level data of the 8 dogs differed significantly from zero bilaterally at around 75 ms at the most posterior sensors. Additionally, we detected differences between the responses to human and dog faces in the posterior sensors at 75–100 ms and in the anterior sensors at 350–400 ms. To our knowledge, this is the first illustration of completely non-invasively measured visual brain responses both in individual dogs and within a group-level study, using ecologically valid visual stimuli. The results of the present study validate the feasibility of non-invasive ERP measurements in studies with dogs, and the study is expected to pave the way for further neurocognitive studies in dogs.

Keywords Electroencephalography · Event-related potential · Dog · *Canis familiaris* · Visual cognition

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Introduction

The ability to recognize faces based on visual cues plays an important role in the social cognition of us, humans (Bruce and Young 1998), and human adults can differentiate faces of their own species better than faces of other species (Tarr and Cheng 2003; McKone et al. 2006). However, face perception is not exclusively a human ability, as several species of non-human animals can discriminate the faces of their conspecifics based on visual cues (for a review, see Tate et al. 2006; Leopold and Rhodes 2010). Recently, dogs' ability to discriminate their own species from others has been studied with various behavioral methods. Dogs can be trained to classify landscape and dog images (Range

et al. 2008), discriminate dog faces from the faces of other species (Autier-Dérian et al. 2013) and discriminate human smiling faces from blank faces (Nagasawa et al. 2011). Dogs have been also found to display species-dependent looking behavior when viewing human and dog faces (Racca et al. 2010; Somppi et al. 2012) and to use a different gaze strategy while viewing human faces compared to dog faces and objects (Guo et al. 2009). Moreover, dogs are able to associate the image of their owner's face with the owner's voice, suggesting that dogs may have an internal representation of their owner's face (Adachi et al. 2007).

Face processing in humans seems to involve face-specific cognitive and neural mechanisms (Tarr and Cheng 2003; McKone et al. 2006). Brain imaging studies have revealed neural circuits in the temporal cortex of the brain, which respond preferentially to faces as opposed to other visual stimuli (Allison et al. 1994; Haxby et al. 1994; Puce et al. 1995; Kanwisher et al. 1997; McCarthy et al. 1997). Similar face-responsive areas have been found in single-unit studies in sheep (Kendrick and Baldwin 1987; Kendrick 1991, 1994) and in non-human primates (Gross et al. 1972; Bruce et al. 1981; Perrett et al. 1982, 1985, 1988; Rolls 1994). The accumulating behavioral evidence suggests specificity of face processing also in dogs, but since similarity of behavior does not necessarily equal similarity in the underlying cognitive brain processes, there seems to be a need for methods suitable for studying dogs' cognitive processes and their neural background in the absence of behavioral responses. Consequently, recent studies of dog brain processing have produced significant advances. The first successful fMRI study of two awake and alert dogs has just been reported (Berns et al. 2012), and in a minimally invasive EEG study sampling event-related potentials (ERPs), dogs' reactions to auditory stimuli were measured with a needle electrode placed at a point along the midline of the dog's head (Howell et al. 2012).

Continuing the advancement of cognitive dog brain research, EEG recording from the surface of the scalp, with adhesive skin electrodes, seems to be another promising method for non-invasive cognitive brain imaging in animals. Although currently widely utilized in scalp-EEG studies of humans, EEG was originally described in intracranial animal studies (Caton 1875). In dogs, EEG has mainly been used for clinical purposes as a diagnostic tool in epilepsy research (e.g., Berendt et al. 1999; Jeserevics et al. 2007; Pellegrino and Sica 2004; James et al. 2011). However, previous EEG studies with animals have mostly been invasive, and they have required sedation or anesthetizing of the animals, which can affect cognitive processing (Koelsch et al. 2006) and limit the topics of study. Non-invasive EEG with undrugged animals has previously been employed in only a few studies: sleep studies with cattle (Hänninen et al. 2008; Ternman et al. 2012) and ERP studies, measuring brain responses to external stimulus events, with chimpanzees (Ueno et al. 2008, 2010; Fukushima et al. 2010).

Various ERP components are well documented in humans and are considered to be good indicators of cognitive and neural processing (Coles and Rugg 1995; for a review, see, e.g., Otten and Rugg 2005). In non-human species, the ERP components have been studied less likely due to differences between human and animal research traditions. However, the event-related potential N1, one of the early ERP components peaking around 100–200 ms after visual stimulus onset, has been characterized both in human non-invasive EEG (e.g., O'Donnell et al. 1997) and in animals with intracranial EEG studies: in monkeys (e.g., Pineda et al. 1994; Woodman et al. 2007) and in dogs (Bichsel et al. 1988; Lopes da Silva et al. 1970a, b). In the current study, we employed a completely non-invasive EEG in assessing the neurocognitive correlates of the visual cognition of dogs. Eight beagle dogs were trained to lie still while the stimulus images were presented on a monitor in front of them, and their brain activity was measured with non-invasive EEG from the surface of the skin. Our aim was to validate the feasibility of non-invasive EEG in studies of dogs by characterizing the visual N1 components in individual dogs as well as within a group-level study. Additionally, to obtain information about the processing related to perceiving different species, we compared the ERP responses of dogs between human and dog faces. Furthermore, since the application of EEG does not harm the dog, or require sedating or restraining of the dog, we set out to establish a methodological basis for studying the ERPs related to dog cognition.

Materials and methods

Subjects

Eight clinically healthy, neutered (two female, six male) purpose-bred beagles participated in the study. Dogs were housed in a kennel-like environment as a social group, with familiar caretakers and daily access to outside exercise area. At the time of the study all the dogs were 4 years old and they weighed on average 12.9 ± 1.9 kg.

The study was performed in strict accordance with the Finnish Act on Animal Experimentation (62/2006) in which the European convention for the protection of vertebrate animals used for experimental and other scientific purposes (Directive 86/609/EEC) is fully implemented. All the experimental procedures of the study were approved by the Finnish National Animal Experiment Board (approval #STH367A/ESLH-2008-04236/Ym-23). In the EEG

measurements, no invasive procedures were applied, and only positive reinforcement was used in the animal training. During the measurements, the dogs were fully alert and conscious at all times with no medication, and neither mechanical nor manual restraint was applied.

Computed tomography acquisition

Prior to EEG data acquisition, computed tomography (CT) images of all dogs were acquired with a Somatom Emotion Duo scanner (Siemens Medical Solutions, Erlangen, Germany) at the Veterinary teaching hospital of the University of Helsinki, in order to visualize the locations of the EEG electrodes with respect to each dog's brains. The electrode positions were indicated with calcium pills placed on the surface of the dog's head, to make the electrode locations clearly visible in the CT scan images. CT scans of the brain were obtained at 2-mm slice intervals: 93 slices were obtained in coronal direction. Prior to the procedure, each dog was sedated with dexmedetomidine (Dexdomitor, Orion Pharma, Finland) 0.15–0.17 ml/kg intramuscularly (i.m.) and butorphanol (Butordol, MSD Animal Health, the United States) 0.15–0.17 ml/kg (i.m.); general anesthesia was induced with intravenous administration of propofol (Vetofol vet, Vet Medic Pharmaceuticals, Finland) 0.5–2.5 ml/kg. Dogs were intubated, and inhalation anesthesia was maintained with isoflurane (Isoflo vet, Orion Pharma, Finland).

Training

The dogs were trained over 18 months, approximately twice a week, for the EEG task. Since muscle movements cause grave artifacts in EEG data, the dogs were trained with positive operant conditioning method (clicker) to lie still on a 10-cm-thick styrofoam mattress and lean their jaw on a purpose-designed u-shaped chin rest for up to 120 s. They were also accustomed to the measurement room and to wear the EEG electrodes and a vest carrying the EEG amplifier (see Fig. 1). The dogs were trained to perform the task on a voluntary basis without commands, and their movements were not restricted during measurements (for more details of the training procedure as previously used with family dogs, see Somppi et al. 2012).

During the EEG recording, dogs lay in the trained position with two experimenters behind a visual barrier in the same room. The dogs were monitored through a webcam (Labtec Webcam 2200), which was placed on top of the monitor.

Stimuli

The stimuli consisted of color images of 36 upright human and 39 upright dog faces, and 3 inverted human and 3 inverted dog faces. Each image was repeated 2–7 times resulting in a total of 240 image presentations (100 human faces, 100 dog faces, 20 inverted human faces and 20 inverted dog faces). The inverted faces were part of a separate study with a different aim, and their small total stimulus number did not result in sufficient signal-to-noise ratio to be comparable to the other categories within the EEG study; however, they did contribute to the general feasibility analysis of the brain responses. The mean size of the face images was 14 % (SD 1 %, ranging between 11 and 18 %) of the size of the monitor (resolution 1,680 × 1,050 px). The face images were approximately 14.6 × 16.0 cm (550 × 600 px, corresponding to the visual field of 12.6° × 13.8°) on the screen, overlaid on a medium gray background of 47.4 × 29.7 cm. All the faces were detached from their original photographic background and placed in the middle of a gray background. The images were acquired from both personal collections and image databases on the internet (e.g., 123rf and bigstockphoto).

Stimulus presentation

The stimuli were presented on a 22″ (47.4 × 29.7 cm) LCD monitor using Presentation® software (Neurobehavioral Systems, San Francisco, USA) at a viewing distance of 0.7 m. Each stimulus was shown for 1.5 s with a 500-ms inter-stimulus interval, during which a blank gray screen was shown. The stimuli were shown in a pseudorandomized order, within 6 stimulus blocks of 8–12 stimuli per block and 2 min 11 ± 10 s (mean ± SEM) rewarding periods between blocks. During the rewarding periods, the dog was rewarded with a food treat and left to settle again on the mattress without being commanded.

The EEG data were gathered in four recording sessions, with 2–5 days in between the measurement sessions. Only one session was recorded per day per dog. On average, the total measuring time of one session was 20 min (ranging between 12 and 39 min). The eye movements of the dogs were simultaneously recorded with an infrared-based eye tracking device (iViewX™ RED, SensoMotoric Instruments GmbH, Germany), which was integrated into the monitor. The eye-gaze data were part of another study with a separate aim.

EEG data acquisition

The EEG data were acquired with an ambulatory Embla® Titanium™-recorder and RemLogic™ 2.0—software (Embla Systems); the trigger system was custom-made for the purpose. The EEG recorder was 3.5 × 7.5 × 11.4 cm in size and 200 g in weight, making it easy for the dog to carry in the vest, and the electrodes were disposable

1) Chin rest
2) Electrodes secured with medical tape
3) Electrode leads connected to the EEG amplifier
4) Vest and a pocket for the EEG amplifier
5) Wires connecting the EEG amplifier to the computer
6) Ground electrode secured with medical tape
7) Mattress

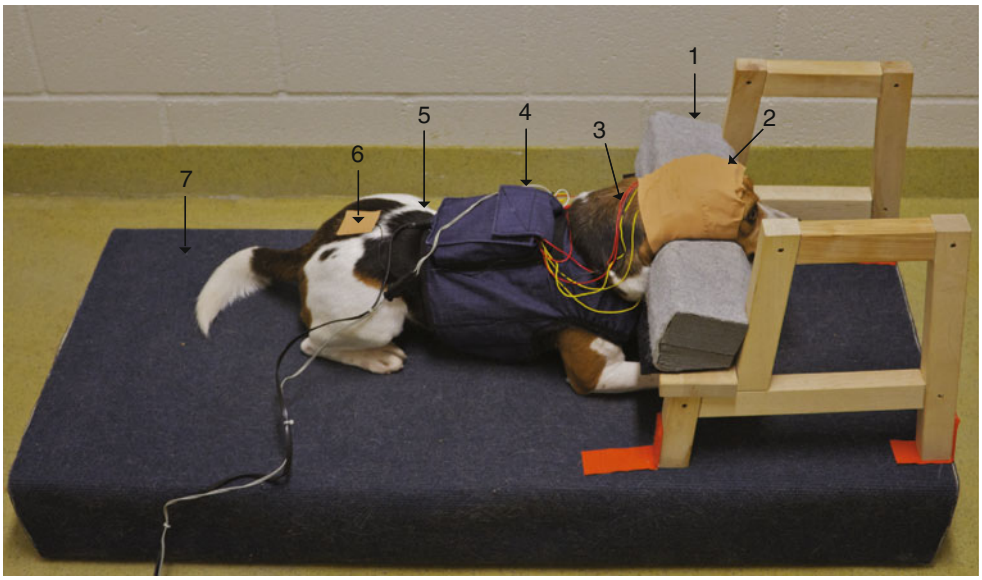

Fig. 1 The experimental setup during the EEG acquisition. The dogs were resting on the styrofoam mattress and leaning their jaw against the chin rest, carrying the dog vest with the EEG amplifier and observing the stimuli from the computer monitor (monitor not visible in picture)

Unilect™ (Unomedical a/s, Denmark) neonatal electrodes with bioadhesive gel and cloth. To attach the electrodes to the skin, the hair from the top of the dog's head was shaved and the skin was rubbed with NuPrep™ gel and cleaned with isopropyl alcohol. Thereafter, drops of cyanoacrylate were applied on the corners of the electrode pads, and the electrodes were attached to the skin. In addition, medical elastic tape was applied on top of the electrodes to ensure their attachment. EEG measurements were obtained with 7 electrodes at the scalp (Fp1 and Fp2 located above the eyes, F3 and F4 located diagonally from the previous in the postero-lateral direction, Cz in the center, and P3 and P4 closest to the dog's neck; see the electrode layout in Fig. 2).

The reference electrodes were placed on the dog's ears and y-linked for a reference, and the ground electrode was placed at the lower back. The EEG signals were band-pass filtered to 0.15–220 Hz and digitized at 512 Hz, and the impedances of the electrodes were measured before, in between, and after the stimulus blocks on each measurement day.

EEG data analysis

The EEG data were analyzed with Matlab R2010B (Mathworks Inc, USA). Before further data analyses, all trials, in which the dog was detected to move, or in which amplitude exceeded 200 μV in any EEG channel, were

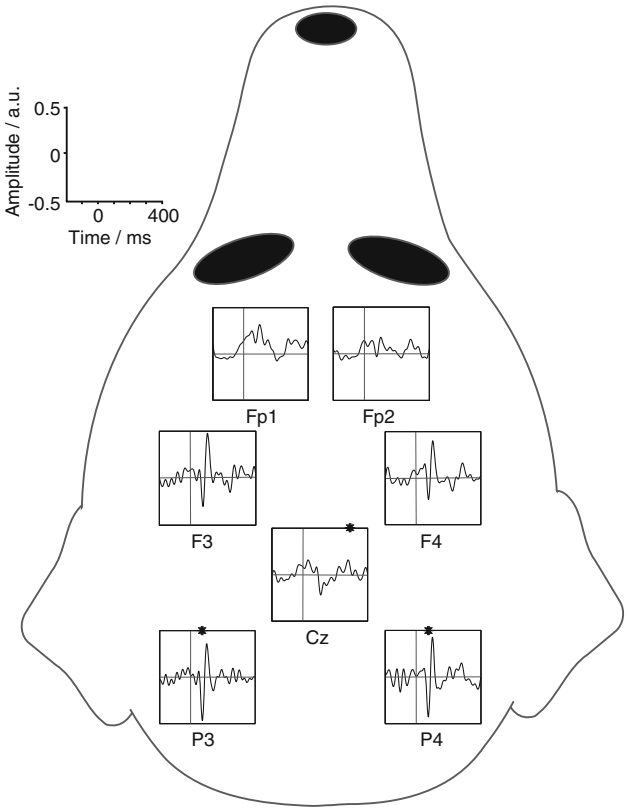

Fig. 2 The electrode layout and the normalized grand-average ERP responses from 8 dogs. The responses that differ statistically from zero at $P < 0.001$ are marked with *asterisks*

Table 1 The normalized grand-average ERP responses from 8 dogs

Channel	Latency (ms)	Amplitude (a.u., mean ± SEM)	*P* value	*t* value	*df*
P3	63.6	−0.21 ± 0.04	0.00085	−5.56	7
	65.5	−0.28 ± 0.05	0.00088	−5.52	7
P4	77.3	−0.43 ± 0.08	0.00072	−5.72	7
	79.2	−0.40 ± 0.08	0.00088	−5.53	7
Cz	282.3	0.15 ± 0.03	0.00042	6.26	7
	284.3	0.15 ± 0.02	0.00019	7.12	7
	286.3	0.15 ± 0.02	0.00022	6.95	7
	288.2	0.14 ± 0.02	0.00055	5.98	7

The EEG channels and time points (latencies), in which the visual evoked brain response differed statistically significantly from zero at $P < 0.001$

discarded to prevent data contamination by muscle movements or external artifacts. Thus, on average, 166 ± 14 (across-dogs mean ± SEM) single trials were included in the final data analysis per dog, ranging from 91 to 209 trials in individual dogs. In the analysis of species-related responses, 66 ± 6 artifact-free trials were acquired to human faces and 67 ± 6 trials to dog faces (across-dogs mean ± SEM). Data sequences included for the analysis had an impedance of approximately 8 ± 3 kΩ (across-dogs mean ± SEM). For each dog, the EEG traces were averaged across single trials from −200 ms prior to 400 ms after the stimulus onset, and low-pass filtered at 30 Hz.

To verify the ERPs statistically at the individual level, a standard deviation was calculated from the baseline period of −200 ms to 0 ms in each EEG channel separately, and the statistical threshold level was set to 3.291 standard deviations (corresponding to the significance level of $P < 0.001$ of the estimated *t* statistics). Thereafter, all the time points from 0 to 400 ms were tested statistically against the baseline level, to reveal brain responses that significantly differ from the baseline level.

For the group analysis of both general ERP response validity and the species-related testing, the responses of individual dogs were normalized with respect to the maximum modulation during the 0–400 ms time period (with respect to the −200 to 0 ms baseline period), by giving the maximum amplitude the value of 1 and scaling the rest of the response accordingly. This was done to scale the responses of all dogs similarly and to prevent the responses of any single dog driving the group-level effect. Thereafter, in the response validity measure, the individual traces were averaged together for a group-level grand average of 8 dogs, and the group-level responses from 0 to 400 ms were compared to zero with one-sample *t* tests ($P < 0.001$). In the species-related testing, ERP traces representing group-level grand averages were calculated separately for the human and dog face categories, and the responses to the human and dog faces were compared using paired-samples t tests with the significance level of $P < 0.01$.

Results

Group-level visual event-related responses

The group-level results of 8 dogs are depicted in Fig. 2; the responses differed statistically at the time points marked with asterisks. The early responses around 65–80 ms differed from zero at the posterior EEG channels P3 and P4. Furthermore, the channel Cz differed statistically from zero at 280–290 ms from the stimulus onset (see Table 1 for details).

The N1 responses of individual dogs

The ERP responses that show the maximum N1 amplitudes in individual dogs are depicted at right in Fig. 3: The dotted lines represent the statistical thresholds calculated from the baseline period of −200 to 0 ms and corresponding to $P < 0.001$ (3.291 standard deviations). The coronal CT sections of the respective dogs' brains are shown at left, illustrating the anterior–posterior section of the head and the brain, above which the channel with the maximum response was located in each dog.

The same form of the ERP response can be seen in all dogs, and all individual dogs showed statistically significant responses at approximately 100 ms at the lateral posterior channels (F3, P3 or P4; see Table 2 for details). Furthermore, in 6/8 dogs, the earlier component at approximately 75 ms also exceeded the statistical threshold; however, there was slight variation in the location of the channel displaying the maximum response. The channel showing the most evident differences between the early 75–100 ms ERP components and the baseline was channel

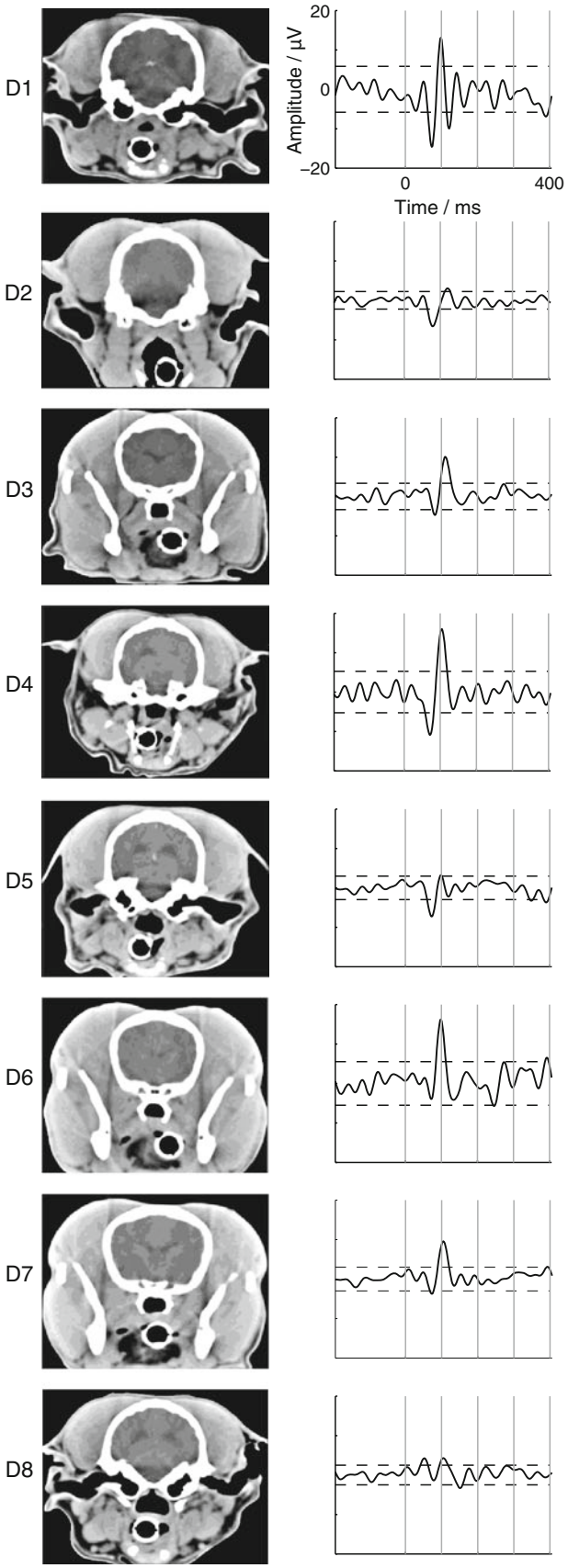

Fig. 3 *Right*: The ERPs of individual dogs from the channels showing the maximum amplitudes of the N1 component. The dotted horizontal lines in the channels illustrate the SD level of 3.291 calculated from the baseline brain activity, corresponding to the *P* value of 0.001. *Left*: individual dogs' computer tomography images from the coronal plane showing the section of the brain above which the channel with the peak amplitude was located

P3 in dogs D1 and D2; channel F3 in dogs D3, D6 and D7; and channel P4 in dogs D4, D5 and D8.

Brain responses related to human and dog faces

Figure 4 depicts the separate ERP responses to the human and dog faces. Significant differences between human and dog face categories were detected at the EEG channels P3, F3 and Fp1. The brain responses within the most posterior/caudal channel P3 differed statistically between human and dog faces at 60–90 ms, the responses within more anterior/rostral channel F3 at 360–370 ms and the responses at the most anterior channel Fp1 at 370–400 ms from the stimulus onset (see Table 3).

Discussion

Visual N1 latency in dogs, monkeys and humans

In this group study of eight dogs, we demonstrated that non-invasive EEG measurement is possible from the surface of the skin in dogs and showed the visual N1 responses of dogs to ecologically valid visual stimuli. In humans, the visual N1 originates in the occipital cortex, and it is part of the normal response to visual stimulation (Allison et al. 1999). The transient form of the dogs' visual N1 response observed around 75 ms seems to resemble the human visual N1 response measured from the scalp, but the response of the dogs appeared earlier than the N1 typically reported in humans. This is in line with previous research, since the N1 component also seems to occur earlier in non-human primates compared with humans, when measured intracranially from the brain (Van der Marel et al. 1984). In a previous intracranial EEG study in anesthetized dogs, the mean latency of the visual N1 peak was approximately 54–56 ms (Bichsel et al. 1988). The early N1 occurrence in monkeys and dogs may be due to the smaller size of their brains compared to humans: The larger human brain has more neurons and synapses, so the information transmitted through human brains has more transmission delays compared to smaller non-human brains (Woodman et al. 2007).

Discrepancies in task variables such as attention and cognitive task may also contribute to the visual N1 latency (Haider et al. 1964; for a review, see Mangun 1995). In our study,

the dogs passively viewed the images without any specific task, whereas in human studies, participants are often given an attentional or memory-related task (see, e.g., Carmel and Bentin 2002). Variables affecting the subjects' attention, such as pre-cueing the upcoming stimulus or attention to a certain spatial location, affect the visual N1 latency and the peak amplitude in humans (Allison et al. 1999; Vogel and Luck 2000). Furthermore, cognitive ERP studies in humans usually have some unpredictability (jitter) in the inter-stimulus interval, but in our study the inter-stimulus interval was constant, which might increase the predictability of the stimulus onset and also affect the corresponding N1.

Response amplitudes and spatial distribution of the early visual responses in dogs

Utilizing a multiple-electrode net instead of a single electrode improves spatial resolution, and in our study, the visual N1 responses were best seen at the posterior/caudal sensors in all dogs. However, the location of the channel showing the maximum response varied slightly in individual dogs. This could be partly due to small anatomical differences between dogs, such as the brain and skull sizes, thickness of the head muscles and their distribution on the skull. Also, a slight variation in the electrode positioning between individuals and impedance differences between the EEG channels or the reference electrodes may have caused variation in the maximum response location across dogs.

Although the latency and the transient form of the response were very similar across dogs, some individual variation was observed in the amplitude of the visual N1 response. This is consistent with findings in human and monkey ERP studies, in which the amplitude of early visual ERPs has also varied across individuals (Luck 2005; Woodman et al. 2007). The folding pattern of the cortex

Table 2 The early visual brain responses from each individual dog

Response	Dog	Channel	Peak latency (ms)	Peak amplitude (μV)	*P* value	*t* value
~75 ms	1	P3	73.4	−14.6	2.2e−16	−8.27
	2	P3	79.2	−6.6	<2.2e−16	−9.80
	3	F3	83.3	−4.7	4.4e−6	−4.59
	4	P4	71.4	−10.9	1.0e−11	−6.80
	5	P4	73.4	−7.3	1.3e−15	−8.00
	6	F3	71.4	−4.0	0.018	−2.36
	7	F3	73.4	−3.8	3.8e−5	−4.12
	8	P4	79.2	−1.4	0.07	−1.80
~100 ms	1	P3	98.8	13.1	1.3e−13	7.41
	2	P3	118.3	3.0	1.1e−5	4.40
	3	F3	110.5	10.1	<2.2e−16	9.88
	4	P4	104.6	16.0	<2.2e−16	10.00
	5	P4	98.8	3.3	0.00034	3.58
	6	F3	98.8	16.2	<2.2e−16	9.69
	7	F3	104.6	9.6	<2.2e−16	10.50
	8	P4	104.6	4.3	1.2e−8	5.70

The EEG channels and time points (latencies), in which the visual evoked brain response differed from the baseline level of brain activity (−200 to 0 ms of the stimulus onset) in each dog. The *P* values of <2.2e−16 indicate extremely significant responses with *t* values over 8.30

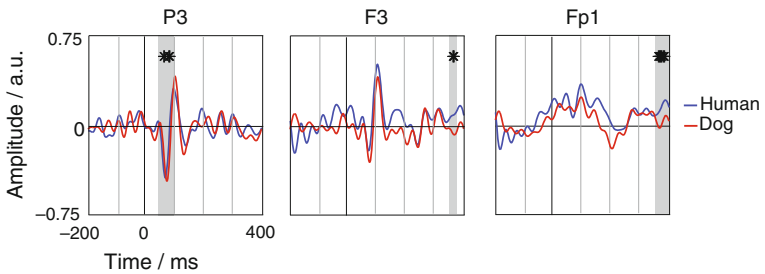

Fig. 4 Normalized grand-average ERP responses to human and dog faces from the channels (*P3*), (*F3*) and (*Fp1*). Responses to human faces are indicated with blue line and the responses to dog faces with red line. The time points, in which the responses to human faces differed statistically significantly (at $P < 0.01$) from the responses to dog faces, are marked with *asterisks*

Table 3 Group-level comparison of the ERPs to human and dog faces

Channel	Latency (ms)	*P* value	*t* value	*df*
P3	59.7	0.0016	−4.99	7
	61.6	0.0012	−5.26	7
	63.6	0.0076	−3.71	7
	81.2	0.0051	4.01	7
	83.1	0.0006	6.10	7
	85.1	0.0008	5.59	7
	87.0	0.0050	4.03	7
F3	364.3	0.0083	3.64	7
	366.3	0.0044	4.14	7
	368.3	0.0032	4.40	7
	370.2	0.0059	3.90	7
Fp1	372.2	0.0078	3.68	7
	374.1	0.0058	3.91	7
	376.1	0.0048	4.1	7
	378.1	0.0045	4.1	7
	380.0	0.0043	4.1	7
	382.0	0.0046	4.1	7
	383.9	0.0056	3.9	7
	385.9	0.0072	3.7	7
	387.8	0.0093	3.6	7
	393.7	0.0068	3.8	7
	395.6	0.0029	4.5	7
	397.6	0.0012	5.2	7
	399.5	0.0027	4.5	7

The EEG channels and time points (latencies), in which the evoked brain responses differed statistically significantly from each other at $P < 0.01$

can vary between individuals, which can affect to the location and orientation of the cortical generator source of ERP components, and influence the amplitude of components measured at a given scalp electrode site (Luck 2005). In addition, the number of averages per individual included in the final data analysis following artifact removal may account for some variations in the amplitude of the responses.

In addition to the early response at around 75 ms, we detected a later response at approximately 100 ms in all individual dogs (see Table 2). The peak latency of this later response varied substantially across dogs, which might be the reason for the lack of statistical significance of this response at the group level.

Visual responses related to species

The early visual ERPs to the images of human faces differed from the responses to dog faces in the most posterior EEG channel P3 at the back of the dog's head, where the early visual cortex of dogs is located (King 1999). However, early ERP components are sensitive to elementary stimulus features such as luminance and contrast and are thus separable from category-specific ERPs, which are sensitive to stimuli of a particular category but not to equiluminant stimuli of another category (see, e.g., Allison et al. 1999; Avidan et al. 2002; Gardner et al. 2005; Kujala et al. 2009). In this feasibility study, the stimuli were chosen to be more ecologically relevant color photos, and the luminance values were not specifically matched across categories. Thus, we cannot rule out the possibility of the early difference between human and dog faces at channel P3 being a consequence of low-level differences between categories. In the future, this should be taken into account in studies concerning early visual responses.

Additionally, we detected later differences between human faces and dog faces at 360–370 ms in the channel F3 and at 370–400 ms in the channel Fp1. The channel F3 was on the side of the dog's head, under which the temporal cortex of the dog's brain is located. The temporal cortex is involved in high-level visual processing of complex stimuli such as faces in humans (Allison et al. 1994; Haxby et al. 1994; Puce et al. 1995; Kanwisher et al. 1997; McCarthy et al. 1997), in monkeys (Gross et al. 1972; Bruce et al. 1981; Perrett et al. 1982, 1985, 1988; Rolls 1994; Tsao et al. 2003, 2006) and in sheep (Kendrick and Baldwin 1987; Kendrick 1991, 1994). The higher visual areas and the later ERP components are suggested to be relatively invariant to contrast changes of the stimuli (Rolls and Baylis 1986; Allison et al. 1999; Avidan et al. 2002); thus, the later difference in ERPs is more likely to be related to categorization of the stimulus images and to the later cognitive processing stages of the faces.

In behavioral studies, dogs gaze at facial images more than object images (Somppi et al. 2012) and display species-dependent looking behavior when viewing human and dog faces (Racca et al. 2010; Somppi et al. 2012). Dogs also seem to gaze differently at human faces compared to dog faces and objects (Guo et al. 2009). Dogs might process human faces differently than faces of other species, because the ability to extract information from human faces and respond appropriately to human facial cues could have been a selective advantage during domestication (Hare et al. 2002; Guo et al. 2009). However, the differences between categories were quite small in our study, which might be due to the relatively small number stimulus images used. Nevertheless, our study has succeeded in setting guidelines for the non-invasive dog EEG, and future studies will further clarify whether the neural mechanisms of face processing in dogs are similar to face processing in the human brain.

The beginnings of dog cognitive neuroscience

Many previous EEG studies in animals have been invasive single-unit recordings and have concentrated on describing the functional characteristics of the individual neurons. In contrast, non-invasive EEG and ERP research in humans has focused on studying the activity of large cell ensembles (i.e., system-level functions) during different cognitive processes. Because of these methodological differences between human and animal EEG studies, the results have been difficult to compare (Woodman et al. 2007; Woodman 2012). Nevertheless, behavioral studies on dogs occasionally make strong connections between dog and human cognitive and social processing. Using solely behavioral methods, we cannot completely resolve whether the underlying neural mechanisms are truly similar across species, or whether the behaviors reminding each other have developed through different mechanisms. Therefore, employing both behavioral and neurocognitive approaches would be beneficial for obtaining a comprehensive view on dog cognitive processes.

Recent studies in the apparently rising field of cognitive neuroscience of dogs have managed to unveil the reward processing in dog brain by the means of fMRI (Berns et al. 2012) and the pre-attentive auditory difference processing of mismatch negativity with needle-electrode EEG (Howell et al. 2012). In human studies, EEG is commonly measured using non-invasive scalp electrodes. However, this technique has rarely been employed with fully alert animals, and it has been considered to be unsuitable for the use in dogs (Howell et al. 2012). The results of our current study expand the dog cognitive neuroscience field by demonstrating the feasibility of fully non-invasive scalp-EEG measurements in both individual and at the group-level study of dogs, based on long and patient positive reinforcement training. The employment of scalp-EEG enables further research into the cognitive functions of dogs and comparative studies of brain processes across species, without harming the animals of study.

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