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Auditory stimulus discrimination recorded in dogs, as indicated by mismatch negativity (MMN)

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ABSTRACT

Dog cognition research tends to rely on behavioural response, which can be confounded by obedience or motivation, as the primary means of indexing dog cognitive abilities. A physiological method of measuring dog cognitive processing would be instructive and could complement behavioural response. Electroencephalogram (EEG) has been used in humans to study stimulus processing, which results in waveforms called event-related potentials (ERPs). One ERP component, mismatch negativity (MMN), is a negative deflection approximately 160–200 ms after stimulus onset, which may be related to change detection from echoic sensory memory. We adapted a minimally invasive technique to record MMN in dogs. Dogs were exposed to an auditory oddball paradigm in which deviant tones (10% probability) were pseudo-randomly interspersed throughout an 8 min sequence of standard tones (90% probability). A significant difference in MMN ERP amplitude was observed after the deviant tone in comparison to the standard tone, $t_5 = -2.98$, $p = 0.03$. This difference, attributed to discrimination of an unexpected stimulus in a series of expected stimuli, was not observed when both tones occurred 50% of the time, $t_1 = -0.82$, $p > 0.05$. Dogs showed no evidence of pain or distress at any point. We believe this is the first illustration of MMN in a group of dogs and anticipate that this technique may provide valuable insights in cognitive tasks such as object discrimination.

1. Introduction

Dog cognition research has increased considerably since the late 1990s (Wynne, 2009) and, in experimental settings, dogs have demonstrated evidence of strong social cognitive skills, such as an ability to effectively communicate with humans (Reid, 2009). Additionally, some dogs can be trained to excel at general cognitive tasks, such as two-dimensional object discrimination (Range et al., 2008) and learning hundreds of words (Kaminski et al., 2004; Pilley and Reid, 2011). In attempting to understand the cognitive abilities of dogs, researchers have tended to rely on behavioural response as the means by which to establish the extent of such skills. While behavioural response is useful for gauging these abilities in dogs, it may be influenced by spurious factors, such as motivation or training levels, which could confound interpretation of experimental outcomes. That is, in cases where dogs fail to succeed at a task, it is possible that they do not lack the ability to pass the test but, instead, lack the desire to do so or an adequate understanding of the task requirements. For this reason, a physiological mechanism for measuring cognitive processing in dogs would be useful to augment behavioural studies.

Electroencephalography (EEG) has been used extensively to research brain functioning in healthy, as well as diseased, populations (Spehlmann, 1981; Basar, 1980). For instance, EEG can be used to examine spontaneous brain activity during sleep versus wakefulness (Choi et al., 1997), which helps researchers understand the effects of disorders like sleep apnoea (Sasse et al., 2005). It is also possible to index the brain's response to a particular stimulus or event. This type of response is called an event-related potential (ERP) (Luck, 2005). In human research, ERPs are waveforms which are related to cognitive processing of stimuli, and are measured in terms of amplitude and latency from stimulus onset (Duncan et al., 2009). Early components, such as the P50 (a positive deflection approximately 50 ms after the stimulus) and the N100 (a negative deflection approximately 100 ms post-stimulus), may represent a

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reflexive response to the stimulus properties, while later components are believed to be related to higher-order processing of the stimulus (Luck, 2005). One of these, called mismatch negativity (MMN), is a negative deflection with a peak in amplitude occurring between 160 and 220 ms after exposure to a novel stimulus (Luck, 2005). For instance, when a subject is listening to a series of identical tones, a tone of a different pitch or volume may elicit MMN (Naatanen et al., 2007). The probability of the differentiated tone affects the presence of MMN (Naatanen et al., 2007); if a differentiated tone occurs less than 20% of the time, MMN is more likely to be elicited than if it occurs 50% of the time. This ERP component is therefore believed to be related to discrimination of an unexpected stimulus in a series of expected stimuli. It may represent change detection from pre-attentive echoic sensory memory (Naatanen et al., 2005, 2007), which is the 'mental picture' that the subject holds of his/her environment (Grivas et al., 2004), reflecting an automatic process which detects the difference between an incoming stimulus and the sensory memory trace of preceding stimuli. In humans, MMN is affected by cognitive disorders such as dementia of the Alzheimer's type (Pekkonen, 2000) and schizophrenia (Catts et al., 1995), as well as alcohol use (Jääskeläinen et al., 1996). It has been implicated in language processing (Pulvermüller et al., 2008), so patients with aphasia have also been studied (Becker and Reinvang, 2007). Because it likely reflects higher-order cognitive processes, such as memory, but can be elicited without the focused attention of the subject, MMN could be a particularly useful instrument in dog cognition research.

Animal studies with ERPs have traditionally focused on understanding the mammalian brain, and have used animals as models of human capabilities when invasive techniques, unable to be used with human subjects, were employed (Buchwald, 1990). Such techniques are not suitable for modern canine cognition research, where the research subjects are generally much loved family pets (Kubinyi et al., 2009) and are not expected to be harmed in any way. The aim of this study was to adapt a minimally invasive ERP recording technique to determine whether MMN could be elicited in pet dogs.

2. Experiment 1

2.1. Methods

The Monash University School of Psychology and Psychiatry Animal Ethics Committee approved this research (AEC number 2010/01-S1). Pet dogs ($n = 10$), ranging from 18 months to 8 years of age, were recruited from metropolitan Melbourne, Australia. They were selected on the basis of owner reports that they were able to settle quickly in novel environments in the presence of their owner, as well as not being distressed while receiving injections during visits to the veterinarian. While there were no specific breed requirements, all dogs were medium to large and had mesocephalic head shapes, rather than long-nosed or short-nosed heads, in order to maintain size and shape standardisation. The participating breeds included: German Shepherd (2), German Shepherd cross, Labrador Retriever, Labrador Retriever x Poodle, Irish Wolfhound cross, Siberian Husky, Standard Poodle, Maremma, and Rottweiler.

All EEG recording took place in a 3 m × 3.3 m sound-attenuated laboratory at Monash University Clayton campus. Dogs were permitted to explore the laboratory for up to 1 h, until they appeared ready to settle on a pet bed placed on the floor. The owner sat on the floor with the dog, or in a chair next to the dog, to maximise relaxation in the dog. Three sterile single-use needle electrodes (Viasys Healthcare Disposable Rapid-Pull 12 mm with 2.5 m cable; San Diego, CA, USA) were inserted underneath the skin of the dog's head in order to obtain an EEG recording. No pharmaceutical sedation was required for needle insertion, and no dog showed any signs of pain or distress during insertion or removal of the needle electrodes, or at any other time throughout the trial.

The recording electrode was placed at Cz, 50% of the distance from the stop (bridge of the nose corresponding to the human nasion) to the external occipital protuberance (bump at the back of the head corresponding to the human inion), caudal to the stop. The ground electrode was placed at Oz, which is 10% of the distance from the stop to the external occipital protuberance, rostral to the external occipital protuberance. The reference electrode was placed on the midline of the neck, 100% of the distance from the stop to the external occipital protuberance, starting from Cz (see Fig. 1). Impedance levels were below 5 kΩ. All electrodes were secured with surgical tape.

A Compumedics Neuroscan Synamps^2 70-channel DC amplifier and Compumedics Neuroscan SCAN 4.5 software (Compumedics Limited, Abbotsford, VIC, Australia) were used to record the dogs' EEG (band pass: 0.1–100 Hz; sampling rate: 500 Hz). Stimuli were delivered using Compumedics Neuroscan Stim 2 software, using a paradigm adapted from Polich (1989). The stimuli were a series of two different tones presented via computer speakers; each tone constituted one trial. The standard tone was 500 Hz and occurred with 90% probability delivered at 48 ± 2 dB. The deviant tone was 1 kHz and occurred with 10% probability delivered at 56 ± 2 dB. The stimuli were presented at this volume to reduce the risk of arousing the dogs with louder stimuli, and are audible according to a dog audiogram (Van der Velden and Rijkse, 1976). All dogs oriented towards the stimuli during the trials, indicating that they could hear the stimuli. The inter-trial interval was 2 seconds, and sequences ranging between 7 and 14 trials were presented consecutively, with 4–5 s breaks between sequences. A total of eight sequences were presented within the first block, seven in the second block, and five in the final block. Three blocks in total were presented with 20 s breaks between blocks. Presentation of the stimuli was pseudo-randomised, with the deviant tone occurring no earlier than the 4th trial in each sequence. The total recording took approximately 8 min, and obtained 200 total trials (180 standards and 20 targets per dog). The maximum time per session was 90 min; however, most dogs finished in less than 1 h. This variation was due to the amount of time required for the dog to fully relax.

After the recording was complete, the needle electrodes were removed and disposed of in a sharps container. The dog received a treat and the owner received a small cash incentive for participation. Two dogs, the German Shepherd cross and the Rottweiler, did not settle in the room within 1 h and the session was terminated without inserting the needle electrodes or obtaining data. We were able to record the EEGs of eight dogs in total.

ERP data were analysed using Compumedics Neuroscan SCAN 4.5 software. EEG blocks with visibly consistent EKG (cardiac activity) or EMG (muscle activity) greater than 50 μV were excluded from analysis. Data from two dogs had to be wholly excluded for this reason. The total number of dogs included for analysis was six. Subsequently, individual data points with amplitude peaks higher than 100 μV were excluded from analysis. There was some variation in the amount of data remaining for each dog following artifact removal. For instance, out of 200 total data points collected per dog, 47 data points were included for one dog, while 185 were included for another. Across all six dogs, a total of 767 artifact free data points were extracted, including 690 for the standard tone and 77 for the deviant tone. Mean amplitudes of all the standard and deviant tone data were extracted and averaged separately for each dog using Compumedics Neuroscan SCAN 4.5 software. The results were then aggregated to produce grand average standard and deviant tone mean amplitudes for the same ($n = 6$). Values are expressed as means, standard errors, and p-values. Peak amplitude detection was established for three components of the deviant and standard