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Using temperature to discriminate in a two-choice task in kea (*Nestor notabilis*)

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Contents

1. Introduction

The physical property temperature is defined as the kinetic energy a matter contains. If the energy of a matter is equal to the energy of the ambient environment, the energy state is in equilibrium. If not, energy will be exchanged from the body with higher temperature to the body with lower temperature (Martinez & de la Peña García, 2013).

Land surface temperatures on earth can range from 80,8°C (Lut Desert, Iran) to up to -110,9°C (Antarctica) (Zhao, et al., 2021). In comparison to this, the life range of body temperatures for animals is very narrow (Schmidt-Nielsen, 1997). Body temperatures of 45-50°C are already lethal for almost all animal life, due to processes such as protein denaturation, thermal coagulation, or inadequate oxygen supply (Schmidt-Nielsen, 1997; Romanovsky, 2018). Similarly, lethal outcomes also occur when body temperatures severely decrease, with most organisms dying at body temperatures of 0°C due to loss of cell function (Schmidt-Nielsen, 1997; Romanovsky, 2018).

1.1. Thermosensation

As there is a constant energy exchange between ambient and body temperatures, it is crucial for an individual to be able to experience temperature in order to keep body temperatures within the optimal range. The ability to perceive temperature is commonly referred to as thermosensation or thermoreception (Castillo, et al., 2018). Thermosensory neurons can be found in the central nervous system (central thermoreceptors) as well as the peripheral nervous system (peripheral thermoreceptors) (Romanovsky, 2018). The majority of central thermoreceptors are warm-sensitive, meaning that they increase their activity when brain temperature increases (Martinez & de la Peña García, 2013; Romanovsky, 2018). Cold-sensitive central thermoreceptors, on the other hand, increase their activity when brain temperature decreases (Martinez & de la Peña García, 2013; Romanovsky, 2018).

While the central thermoreceptors are activated by the brain temperature of an individual, the peripheral thermoreceptors react to the skin surface temperature. They exhibit a, for sensory neurons typical, phasic-tonic discharge pattern, with a continuous discharge of nerve impulses when skin surface temperatures are constant (tonic response), and a rapid increase or decrease of discharge when skin surface temperatures change (phasic response) (Martinez & de la Peña García, 2013). The majority of peripheral thermoreceptors are cold-sensitive with warm-sensitive thermoreceptors being less common (Romanovsky, 2018). The thermosensitive elements of the peripheral thermoreceptors are the transient receptor potential

channels, short TRP channels (Venkatachalam & Montell, 2007; Romanovsky, 2018). However, in case skin surface temperatures reach an injurious level, thermal perception is taken over by nociceptors, thereby inducing the sensation of pain (Martinez & de la Peña García, 2013).

In mammals, the TRP channels TRPV1 (subfamily: vanilloid) and TRPV2, have been observed to be activated by temperature levels above 43°C and 52°C, respectively (Venkatachalam & Montell, 2007). Further, TRPV3 and TRPV4 were activated at moderate temperatures of 33-39°C and 27-34°C (Venkatachalam & Montell, 2007). The sensation of low temperatures is facilitated through the channel TRPM8 (subfamily: melastatin), which reacts to temperatures beneath 28°C (Pedersen, et al., 2005; Venkatachalam & Montell, 2007). TRPV1 and TRPM8 have also been found to react to similar temperatures in other vertebrates (frog, chicken, teleost fishes), although temperature ranges for activation might differ depending on the species (Myers, et al., 2009; Saito & Tominaga, 2015; Clark & Smeraski, 2022). The presence of the TRP channels in the peripheral nervous system of mammals and other vertebrates not only facilitates the perception of ambient temperatures, but in theory could also allow non-human animals to discriminate between varying perceived ambient temperatures.

1.2. The relevance of ambient temperature

Another reason that might suggest why it is in favour for non-human animals to be able to discriminate between varying ambient temperatures is the profound effect ambient temperature seems to have on animal behaviour. It was found, for example, that the willow tit (*Poecile montanus*) and the goldcrest (*Regulus regulus*) change their foraging behaviours in winter according to the ambient temperature (Alatalo, 1982). Particularly in the latter, hovering motions decreased with lower ambient temperatures and got replaced with non-hovering foraging behaviours such as hopping (Alatalo, 1982). Similar results were found in two species of hummingbirds (*Calypte anna*, *Selasphorus rufus*), who decreased non-feeding flights with decreasing temperatures (Beuchat, et al., 1979), as well as in four wintering woodland bird species (*Picoides pubescens*, *Parus carolinensis*, *Baeolophus bicolor*, *Sitta carolinensis*), who increased time stationary and decreased total distance travelled with decreasing temperatures (Grubb, 1978). Decreases in flight activity were also found in the California myotis (*Myotis californicus*) and the common noctule bat (*Nyctalus noctula*), while other species of bats, such as the pallid bat (*Antrozous pallidus*) and the common pipistrelle (*Pipistrellus pipistrellus*), ceased nocturnal foraging flights altogether when temperatures fell under 10°C and 5°C,

respectively (Erkert, 2000). Moreover, Yunnan snub-nosed monkeys (*Rhinopithecus bieti*) decreased their daily path lengths (Baoping, et al., 2009), and black howler monkeys (*Alouatta pigra*) (Aristizabal, et al., 2018), golden snub-nosed monkeys (*Rhinopithecus roxellana*) (Sha, et al., 2020), two species of macaques (*Macaca nemestrina*, *Macaca silenus*) as well as white-fronted capuchins (*Cebus albifrons*) (Hou, et al., 2020) were observed to decrease their activity overall and increase resting with decreasing ambient temperatures.

Further, Caraco and colleagues (1990) observed that yellow-eyed juncos (*Junco phaeonotus*) adopted a more risk-prone foraging strategy when ambient temperatures were low, by preferring a high variance reward, compared to more risk-averse strategies with a preference for low variance rewards when ambient temperatures were high (Caraco, et al., 1990). In contrast to these findings, Bateson (2002) observed that European starlings (*Sturnus vulgaris*) preferred to engage in risk-averse strategies despite low ambient temperatures (Bateson, 2002). Comparable results of risk-aversion were also found in Japanese macaques (*Macaca fuscata*) (Enari & Sakamaki-Enari, 2013).

Remarkably, ambient temperature was also observed to influence the migration and singing behaviour of birds. Low ambient temperatures in autumn, for example, evoked nocturnal migratory restlessness (*Zugunruhe*) in white-throated sparrows (*Zonotrichia albicollis*), a short-distance migrant, and, further, the amount of restlessness displayed increased the lower ambient temperatures were (Berchtold, et al., 2017). Similar results were found in the northern wheatear (*Oenanthe oenanthe*), a long-distance migrant (Klinner & Schmaljohann, 2020). The northern wheatear increased nocturnal migratory restlessness when temperatures at their stopover site decreased, and migratory restlessness decreased when temperatures increased (Klinner & Schmaljohann, 2020).

The start of dawn singing was found to be delayed with high ambient temperatures in Alström's warbler (*Phylloscopus soror*), streak-breasted scimitar babbler (*Pomatorhinus ruficolli*), brownish-flanked bush warbler (*Cettia fortipes*) (Puswal, et al., 2021), and American robin (*Turdus migratorius*) (Bruni, et al., 2014). Interestingly, other species such as the song sparrow (*Melospiza melodia*) (Bruni, et al., 2014), the European robin (*Erithacus rubecula*) (Thomas, 1999) the Eurasian wren (*Troglodytes troglodytes*) (Garson & Hunter, 1979) and the great tit (*Parus major*) (Garson & Hunter, 1979; Naguib, et al., 2019) were observed to sing earlier with higher ambient temperatures and to delay the start of dawn chorus when ambient temperatures were low. The song rate of Alström's warbler and brownish-flanked bush warbler decreased

with higher temperatures (Puswal, et al., 2021), while the song rate of Carolina wren (*Thryothorus ludovicianus*) (Strain & Mumme, 1988) and the pied flycatcher (*Ficedula hypoleuca*) (Gottlander, 1987) increased with higher ambient temperatures.

1.3. Temperature as non-visual property

Under normal circumstances, the physical property temperature is a non-visual or invisible property of an object and cannot be perceived with the naked eye such as colour, size or shape. This is due to the electromagnetic radiation emitted by a matter at non-zero temperature having a wavelength range between 0,1 to 100µm, which is predominantly within the infrared (IR) range of approximately 0,7µm (700nm) and higher (Meseguer, et al., 2012). In comparison to this, the peak wavelength of the longwave-sensitive (LWS) cone opsin of mammals and birds, for example, only resides around 0,5 to 0,57 µm (500-570nm), which does not overlap with the wavelength range of IR (Goldsmith, 2006; Hunt, et al., 2009). Consequently, the characteristics of an invisible property have to be perceived with other senses including touch, smell or taste.

Exceptions have, however, been found in some species which are able to detect thermal energy without directly interacting with an object. Crotaline snakes (pit vipers) as well as some species of the families *Pythonidae* (python) and *Boidae* (boa), for example, possess IR pit organs in their facial region which enable them to effectively detect and locate their prey, particularly in the absence of light (Campbell, et al., 2002). The pit organ is presumed to contrast deviations from the surrounding temperature produced by the body temperature of their warm-blooded prey animals in the snake's field of view and combines this IR image with the visual image perceived by the eyes themselves (Campbell, et al., 2002). The range of the thermal radiation detection reaches approximately 60cm in Crotaline snakes and 30cm in species of the python and boa family, and are presumably most important during strike towards the prey (Campbell, et al., 2002). Analysis of the pit organ have shown higher expressions of the warm-sensitive TRP channel TRPA1 (subfamily: ankyrin) within the organ tissue, which is assumed to be the source of IR detection in snakes (Saito & Tominaga, 2015).

Comparable thermal detection was also found in the common vampire bat (*Desmodus rotundus*), who specializes on feeding on warm-blooded vertebrates such as bovines (Kürten & Schmidt, 1982). Similar to the organ of their reptilian counterparts, the tissue of the vampire bat pit organ shows an increased expression of a TRP channel, in this case TRPV1 (Gracheva, et al., 2011; Saito & Tominaga, 2015). The warm-sensitive TRPV1 channel, additionally, shows

an alteration in activation threshold of 30°C compared to 43°C in other mammals and can be found within the nasal tissue of the vampire bat (Kürten & Schmidt, 1982; Gracheva, et al., 2011). The range of the mammalian pit organ reaches a distance of 16cm and is presumed to help select suitable biting sites (Kürten & Schmidt, 1982). The combination of IR images with visual images is presumably implemented in a similar way as found in IR-sensitive snakes (Campbell, et al., 2002).

Besides the pit organs found in vertebrate species, certain invertebrates have been found to be able to detect thermal radiation from a distance as well. Several species of the genus *Melanophila* (*Buprestidae*), including the black fire beetle (*Melanophila acuminata*), specialize on laying their eggs in the bark of freshly burned-out conifers right after a forest fire (Campbell, et al., 2002). The beetles possess one IR-sensitive thermo-mechanical receptor located on each side of their thorax, also referred to as pit organ, which further consists of 50-100 sensory organs called sensilla (Campbell, et al., 2002). The sensilla within the pit organ expand through the absorption of IR, which then triggers a nerve impulse in the sensory system of the beetle (Campbell, et al., 2002). This means that, unlike in snakes and vampire bats, IR is detected photomechanically instead of through the activation of TRP channels (Campbell, et al., 2002). With their pit organs the beetles can detect forest fires from a distance of 12km and, moreover, have been observed to adopt more favourable leg positions during flight to enhance the detection of an IR source (Schmitz & Bleckmann, 1998).

Thermal radiation detection was also found on the antennal tips of leaf-cutting ant workers (*Atta vollenweideri*) in form of cold-sensitive sensilla (Ruchty, 2010). With the help of their thermosensitive sensilla, the ant workers were observed to consistently prefer a thermal source 5°C above the ambient temperature when presented in a two-choice task and, therefore, reliably discriminated between temperature to solve the task (Ruchty, 2010). Although it is still unknown how exactly the ants perceive the temperature, Ruchty (2010) proposed an involvement of the TRP channel family (Ruchty, 2010).

This shows that non-human animals, with the ability to detect the physical property temperature without close proximity, are able to discriminate between temperatures. However, as mentioned before, these examples remain the exception as for the rest of the non-human animals the physical property temperature is invisible and can only be perceived through close proximity or touch. So far, no study has investigated whether those non-human animals are

also able to discriminate between temperatures. Nonetheless, the investigation of other invisible properties has led to promising results in the last decades.

One of the first studies investigating invisible properties was conducted by Klüver (1933), who successfully trained monkeys to discriminate between two boxes differing in the invisible property weight (Klüver, 1933). A similar study was performed with chimpanzees (*Pan troglodytes*), who learned to discriminate between a visually identical heavy and light box (McCulloch, 1941). In another experiment with bonobos (*Pan paniscus*), orangutans (*Pongo pygmaeus abelii*) and gorillas (*Gorilla gorilla gorilla*), the subjects were trained to exchange an object with a certain weight (either heavy or light) for a reward (Schrauf & Call, 2009). Five out of 12 subjects reliably chose the correct weight after a median of 331 trials (Schrauf & Call, 2009). Similar results were found in Goffin's cockatoos (*Cacatua goffiniana*), who reliably discriminated between visually identical heavy and light objects after an average of 60,6 trials (Lambert, et al., 2021). The Goffin's cockatoos learned to discriminate between weights faster when an additional visual cue was added (average: 40,8) (Lambert, et al., 2021). Moreover, there is evidence that New Caledonian crows (*Corvus moneduloides*) as well as kea (*Nestor notabilis*) discriminate between objects of differing weight as well and, further, that former are able to infer the weight of objects (Lambert, et al., 2017; Jelbert, et al., 2019).

Promising results were also found investigating the invisible property odour. In the study by Roper (2003) yellow-backed chattering lories (*Lorius garrulus flavopalliatus*) were observed to discriminate between visually identical objects through odour cues (Roper, 2003). The subjects were presented with scented and unscented dispensers, of which only former contained a food reward, and learned to reliably choose the scented dispenser while at the same time avoiding the unscented dispenser (Roper, 2003). Similarly, the kakapo (*Strigops habroptilus*) has been observed to consistently choose an opaque bin containing food over an empty bin by discriminating between their scents (Hagelin, 2004), while kea and kaka (*Nestor meridionalis*), two other members of the family *Nestoridae,* were able to discriminate between different odours and changed behaviours with increasing concentrations (Gsell, et al., 2012). Moreover, birds of prey (*Vultur gryphus*, *Haliaeetus leucocephalus*, *Aquila chrysaetos*, *Aegypius monachus*, *Sarcoramphus papa*) have been found to associate an artificially added scent (peppermint oil) with food packages and reliably chose visually identical empty packages containing the associated scent over empty packages without any scent (Nelson Slater & Hauber, 2017).

Since many studies have shown that certain species are able to discriminate between invisible properties in general, the aim of this master's thesis was to explore whether an animal, the kea, who proved to be able to discriminate both weight and odour, is able to discriminate the invisible property temperature as well.

1.4. Kea parrots

The kea is a large parrot endemic to the mountainous areas of the South Island of New Zealand (Brejaart, 1988; Diamond & Bond, 1999). Individuals generally occur at altitudes between 600-2.000m above sea level (asl) and can be found in open countryside, grassland, subalpine shrubland as well as forest, with the interface of forest and alpine grassland zones at heights of 1.250-1.500m asl being most frequented (Brejaart, 1988). The high altitudes of the natural habitat give constant rise to harsh weather activities and low temperatures. At the valley floors, even in midsummer, daily maxima only reach around 20°C and snow may fall at altitudes above 1.500m asl, while in winter daily minima may reach around -2°C and heavy snow- or rainfalls are very likely (Diamond & Bond, 1999).

As was found in many other species, also kea have been observed to change their behaviour according to the ambient temperature. Diamond & Bond (1999), for example, have observed that wild kea stay longer at foraging sites in the morning and return earlier in the afternoon when ambient temperatures were low (Diamond & Bond, 1999). When ambient temperatures were higher, kea left their foraging sites already in the early morning hours and did not come back until sunset (Diamond & Bond, 1999). Moreover, Jackson (1963) noticed that kea preferred to build their nests at locations with higher ambient temperatures and direct access to sunlight (Jackson, 1963).

Based on the literature suggesting that ambient temperature influences the behaviour of kea (Jackson, 1963; Diamond & Bond, 1999), that birds possess TRP channels (Saito & Tominaga, 2015) as well as that kea are able to discriminate the invisible properties weight (Lambert, et al., 2017) and odour (Gsell, et al., 2012), they appear to be a very promising model to test the ability of temperature discrimination.

1.5. Hypothesis and predictions

In this experiment kea were, at first, trained to associate a target temperature with a food reward. After training, the subjects continued with test 1, a two-choice task, inspired by the studies investigating other invisible properties (Schrauf & Call, 2009; Gsell, et al., 2012;

Lambert, et al., 2021), in which the kea were presented two visually identical apparatuses. One of both apparatuses held the target temperature experienced during training and a hidden food reward. It was hypothesized that:

Test 1:

H_1: The temperature will affect the choice of kea in the two-choice task.

H_0: The temperature will not affect the choice of kea in the two-choice task.

It was predicted that the kea will follow the target temperature to retrieve the reward reliably. Moreover, since kea are assumed to be unable to visually perceive temperature (Goldsmith, 2006; Hunt, et al., 2009), it was expected that their first approach of an apparatus will be random, due to the visual identity of the two apparatuses. It was predicted that in case the subject approached the apparatus which did not contain the target temperature first, they will switch to the other apparatus.

In a second test (test 2) the subjects were presented one apparatus with two compartments. One of the two compartments held a hidden reward depending on which temperature the apparatus contained. Again, it was hypothesized that:

Test 2:

H_1: The temperature will affect the choice of kea.

H_0: The temperature will not affect the choice of kea.

It was predicted that the subjects will follow the temperature cue to retrieve the reward reliably. It was not expected that subjects will switch between compartments (as expected in test 1) as both compartments were located on the same apparatus and the reward could be accessed as soon as the subject approached the apparatus. However, in case switches did occur, it was predicted that the subject will switch from the unrewarded compartment towards the rewarded compartment. Additionally, it was predicted that as the subjects associated the temperatures with the rewarded compartment in the course of test 2, the subjects will choose the correct compartment more often and faster as test 2 progressed.

2. Material and Methods

This study was approved by the Ethics and Animal Welfare Committee of the University of Veterinary Medicine, Vienna, in accordance with the University's guidelines for Good Scientific Practice (ETK-042/02/2022). Training and testing took place at the Haidlhof Research Station, Bad Vöslau (Lower Austria), between April 2022 and July 2022.

2.1. Subjects

Six female and six male adult kea parrots (*Nestor notabilis*), between the age of four and 18 years were trained and tested throughout the course of this study (Tab. 1). The subjects were part of a larger flock consisting of 23 kea and were housed in a 52m x 10m x 4m outdoor aviary. The aviary provided various enrichment elements such as foraging and hiding opportunities, perches, as well as two artificial ponds (Fig. 2). Additionally, the aviary could be separated into smaller, isolated areas through sliding gates including the compartments where training and testing took place. The birds received well-balanced meals consisting of fruits, vegetables, grains and protein three times a day. Drinking water was provided *ad libitum*.

Table 1: Name, abbreviation (abbr.), sex, year of hatching, time slot for training/testing (group), as well as the assigned target temperature during test 1 (test 1) and the temperatures assigned to the according compartment sides (from the subject's point of view) during test 2 (test 2) of every subject. The subjects *Mali and **Papu were excluded as the study progressed.

name	abbr.	sex	hatched	group	test 1	test 2
Diana	Di	female	2017	afternoon	4°C	40°C left; 4°C right
Jean-Luc	Je	male	2015	morning	40°C	40°C left; 4°C right
Kermit	Ke	male	2004	morning	40°C	4°C left; 40°C right
Mali*	Ma	female	2014	afternoon	40°C	4°C left; 40°C right
Papu**	Pu	female	2013	morning	40°C	40°C left; 4°C right
Pancake	Pn	male	2017	morning	4°C	4°C left; 40°C right
Paul	Pa	male	2010	afternoon	40°C	40°C left; 4°C right
Pick	Pi	male	2004	morning	4°C	40°C left; 4°C right
Plume	Pl	female	2007	afternoon	40°C	4°C left; 40°C right
Skipper	Sk	male	2017	afternoon	4°C	4°C left; 40°C right
Sunny	Sy	female	2007	afternoon	4°C	40°C left; 4°C right
Tai	Ti	female	2018	morning	4°C	4°C left; 40°C right

2.2. Apparatus

Two identical wooden apparatuses were used for this experiment. Each apparatus consisted of two screwed segments, one 21,5cm x 21cm x 8cm wooden platform and an adjacent 12cm x 12cm x 33,5cm wooden tower (Fig. 1e). In addition, the top of the tower was restricted by three 12cm x 7cm opaque, plastic barriers which blocked access to the top, except for the side which was facing the platform. During training 1A, training 1B and test 1 there was one 1cm deep compartment located at the centre of the top of the tower (Fig. 1a). During test 2 the top of the tower held two symmetrically placed 1cm deep compartments (Fig. 1b).

Figure 1: a) the apparatus used during training 1A, training 1B and test 1 with one grey plastic lid (basic lid) closing the top compartment and a pad mounted on the platform (pink). b) the apparatus used during test 2 with two grey plastic lids (metal washer lid) closing the top compartments and a pad mounted on the platform. c) basic lid with the ring bolt screw at the top and the plastic part at the bottom. d) metal washer lid with the ring bolt screw at the top, followed by the metal washer and the plastic part at the bottom. e) sketch with measurements of the apparatus.

The compartments were used to hide a food reward (one quarter of a peanut) during certain phases of the experiment by closing it with plastic lids (detailed description in section 2.4 Procedure, p. 12). During training 1A, training 1B and test 1 six identical grey plastic lids with a ring bolt screwed through the centre (hereinafter basic lid) were used to close the compartment at certain steps with a tight fit (Fig 1c). The tight fit ensured that the subject could not open the basic lid by accident but had to pull with force to reveal the compartment underneath it. During test 2 ten identical grey plastic lids with a ring bolt screwed through the centre and a metal washer embedded between the plastic and screw were used (hereinafter metal washer lid) (Fig 1d). Due to the metal washer's rigidity the metal washer lid was more loose-fitted than the basic lid and could be removed with a light pull. Furthermore, four identical pink heating pads (hereinafter pads) from SnuggleSafe with a diameter of 20cm were used (Fig 1a, 1b).

During the experiment the subject was supposed to step on the apparatus thereby experiencing the temperature of the mounted pad with their feet before interacting with the basic lid during training 1A, training 1B and test 1 or the metal washer lid during test 2 to reveal the compartment underneath it. The pads were either heated-up in the microwave at 550 watts for 8 minutes to an innocuous temperature of around 40°C (noxious levels in bird extremities were found to be at 50 to 53°C (Hau, et al., 2004)) or cooled down in the freezer to approximately 4°C, an ambient temperature regularly experienced by kea in winter. Additionally, the metal washer lids used in test 2 were also either heated-up to approximately 40°C with hot water or cooled down to 4°C with ice water, which the subjects experienced with their beak when interacting with the metal washer lid. The details on when which temperature was used is described in the section 2.4 Procedure (p. 12).

2.3. Setup

Training and testing of all subjects were mainly carried out in the test compartment located to the left when entering the main aviary (*Porticula tabula*, *Porticula spectans*; short PO), except for Tai (Ti), who preferred to be trained and tested at the compartment located to the right (*Porticula res*, *Porticula expectatio*; short PA) (Fig. 2).
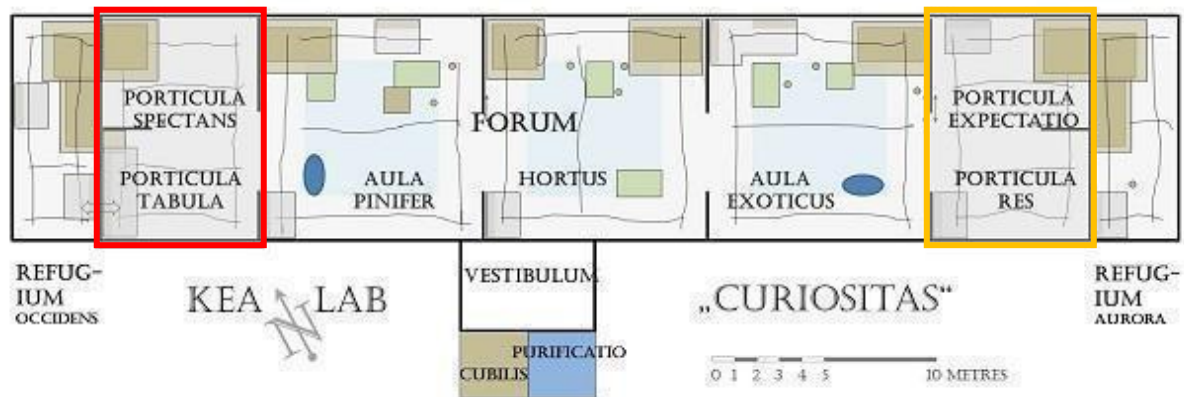

Figure 2: Map of the entire aviary. The main aviary (forum) could be accessed through the vestibulum. The test compartment PO located at the left is indicated in red, the test compartment PA located at the right is indicated in yellow. *Porticula spectans* and *Porticula expectatio* of the respective test compartments were used as waiting area. *Porticula tabula* and *Porticula res* were used as training/testing area.

During the experiment the area *Porticula spectans* (7m x 5m x 4m) of the test compartment was used as waiting area (*Porticula expectatio* in PA) for the subject and the area *Porticula tabula* (7m x 5m x 4m) was used as training/testing area (*Porticula res* in PA). Waiting and

training/testing area could be separated through a sliding gate. Furthermore, the entire test compartment (waiting and training/testing area) could be visually isolated from the main aviary (forum) through opaque, white sliding panels to prevent other birds from interfering or peeking.

Within the training/testing area the apparatus was placed vis-à-vis to where the sliding gate opened to the waiting area, with the platform of the apparatus facing the gate. During training 1A, training 1B and test 2 the distance between apparatus and sliding gate was 240cm. During test 1 two apparatuses were placed with a distance of 250cm to the gate and 115cm to one another. All training and test sessions were recorded using a JVC camcorder (MODEL No.:GZ-RX625BE) located at the left corner of the training/testing area adjacent to the waiting area. Additionally, two buckets of water, in which the metal washer lids were cooled down or heated-up, were placed next to the camcorder during test 2.

2.4. Procedure

Each subject received one session of training or testing per day three times a week. One exception was made for the subject Kermit (Ke) who received the third session (in the morning) and forth session (in the afternoon) of test 2 (detailed description of test 2 in section 2.4.4 Test 2, p. 16) on the same day. One session consisted of ten trials (except for session 7 of test 2 of the subject Je which only consisted of nine trials due to an error). The birds were called individually and at random order into the waiting area of the test compartment and were released back into the main aviary after the session was completed. Participation in this study was voluntary for all 12 birds at any given time. If the subject did not enter the waiting area when instructed to do so on several occasions they were not trained or tested on this specific day. Likewise, if the subject stopped participating during training or testing the session was stopped immediately and the subject was released back into the main aviary.

2.4.1. Training 1A

All subjects started with training 1A. Birds were separated into two groups, which were maintained throughout the entire experiment. One half of the subjects were trained in the morning (morning group: Je, Ke, Pi, Pn, Pu, Ti), from 10 am to 12 pm (Tab. 1). The other half were trained in the afternoon (afternoon group: Di, Ma, Pa, Pl, Sk, Sy), from 1:30 pm to 3:30 pm (Tab. 1), in order to keep ambient temperatures as similar as possible to minimize the impact on the experiment.

During training 1A the subject was familiarized with the apparatus (Fig. 1a), and trained how to correctly interact with the apparatus and the basic lid using a stepwise process and rewards. Throughout the entire training 1A a pad was mounted on the apparatus. For six birds (Je, Ke, Ma, Pa, Pl, Pu) the heated-up pad was mounted on the apparatus, meaning that their target temperature was 40°C (Tab. 1). The remaining six birds (Di, Pi, Pn, Sk, Sy, Ti) were trained with the cooled down pad mounted on the apparatus. Their target temperature was 4°C (Tab. 1). The aim of training 1A was for the subject to associate the target temperature mounted on the apparatus with the reward.

In the first step of training 1A the subject was trained on how to correctly step onto the apparatus to ensure they experienced the temperature of the pad mounted on the platform with their feet. For that purpose, the experimenter stood behind the apparatus facing the sliding gate. With their hand the experimenter was hovering the reward over the pad until the subject approached the apparatus from the front. When the subject stepped or hopped onto the pad, thereby experiencing their target temperature, the experimenter placed the reward in front of the compartment on top of the tower (Fig. 3a). After claiming the reward, step 1 was successfully completed and the experimenter continued with step 2. Between each trial the subject was sent back into the waiting area while the apparatus was prepared for the next trial. In step 2, the experimenter visibly placed the reward behind the compartment on top of the tower (Fig. 3b). If the subject was not attentive the experimenter addressed them with their name. Then the subject was allowed into the training area to retrieve the reward. The reward was correctly claimed if the subject stepped or jumped onto the pad and hence felt their target temperature before retrieving the reward. If the reward was retrieved in any other way, for example by directly jumping on top of the tower which meant that the subject was not able to feel the temperature of the pad, step 1 was repeated in the following trial. Once the subject correctly retrieved the reward in three consecutive trials the experimenter continued with step 3. During step 3 the experimenter visibly placed the reward inside the compartment on top of the tower (Fig. 3c). Once the subject correctly claimed the reward in three consecutive trials the experimenter continued with the fourth and last step of training 1A. For the last step the experimenter visibly placed the reward inside of the compartment on top of the tower before closing it with a basic lid (Fig. 1c; Fig. 3d). Training 1A was completed once the subject correctly retrieved the reward in step 4 for one entire training session (10 trials). After completing training 1A the subject continued with test 1.
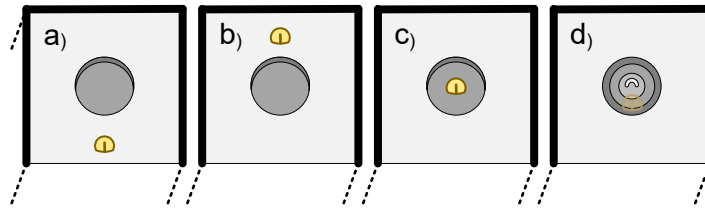
Figure 3: a) reward (indicated in yellow) placement on top of the tower during step 1 of training 1A. b) during step 2. c) during step 3. d) during step 4.

Before and after each session the temperature of the pads mounted on the apparatus was measured using a BOSCH UniversalTemp 3 603 F83 100 infrared thermometer. Additionally, the ambient temperature was measured in front of the apparatus before each session.

2.4.2. Training 1B

A subject underwent training 1B in case set criterion was not met during test 1, as it suggested that the bird has not associated the target temperature with the reward. Therefore, an alteration of step 4 of training 1A was repeated for three sessions per bird. The same apparatus as in training 1A was used throughout the entire training 1B for all birds.

During training 1B the subject experienced the target temperature mounted on the apparatus in 5/10 trials per session as well as a non-target temperature mounted on the apparatus in the remaining five trials per session. The non-target temperature of a subject was the opposite of which was assigned to them, meaning that for birds who got rewarded for 40°C the non-target temperature was 4°C, and vice versa. The order in which the temperatures were mounted on the apparatus was semi-randomized. One temperature was not used more than two trials in a row and the temperature of the first and second trial of a session was never the same. Only the target temperature was rewarded. The baiting process during training 1B was not visible for the subject. Two opaque, white barriers (barrier 1: 205,5cm x 50cm; barrier 2: 100cm x 52cm) were placed in front of the apparatus in form of an L-shape to block the view. In case the non-target temperature was mounted, the apparatus was pseudo-baited to avoid differences in baiting time. Before the barriers were removed and the subject was allowed to approach the apparatus, the mounted pad was wiped with a towel to avoid any visual cues, such as condensation. After completing three sessions of training 1B the subjects repeated test 1. The aim of training 1B was for the subject to associate or further associate the target temperature with the reward through more experience with their target temperature as well as by giving a contrast, the non-target temperature, which lead to no reward.

2.4.3. Test 1

After completing training 1A the subjects continued with test 1. During test 1 the subject was exposed to two visually identical apparatuses in a two-choice task. Both apparatuses were holding a pad, one containing the target temperature and the other the non-target temperature. The apparatus used for training 1A and training 1B was always positioned on the left side (from the subject's point of view). The side of the target and non-target temperature was semi-randomized. In 5/10 trials the pad containing the target temperature was mounted on the right apparatus and in the remaining five trials it was mounted on the left apparatus. One temperature was not mounted on the same side more than two trials in a row. Further, the temperature for the first and second trial was never mounted on the same side. The ambient temperature was measured in the middle of both apparatuses before each session.

Only the apparatus with the target temperature mounted was baited with a reward, while the non-target temperature was pseudo-baited. The baiting process was not visible for the subject and the baiting procedure was identical for every trial. After placing the opaque, white barriers, the experimenter mounted the pads, thereby always starting with the apparatus on the right side (from the subject's point of view). Both pads were wiped with a towel to remove any visual cues. Then the experimenter continued with baiting or pseudo-baiting the reward by placing it inside of the compartment on top of the tower before closing it tightly with a basic lid. Again, always starting with the apparatus on the right.

After baiting the subject was allowed into the testing area to choose one of both apparatuses. A choice was made once the subject moved the basic lid to an extent where the compartment underneath was revealed and hence also the presence or absence of a reward. The subject was allowed to step on top of the pads and experience the temperature of both apparatuses before making a choice, since the location of the target temperature and hence the reward had to be experienced directly and could not be assessed by any visual cues. If the subject first approached one apparatus without interacting with the basic lid in a way that revealed the presence or absence of a reward and then moved towards the other apparatus and interacted with the basic lid in a way that did reveal the compartment underneath it, this behaviour was interpreted as a switch. After the choice was made, the subject was allowed to retrieve the reward if they chose the apparatus mounted with the target temperature before being sent back into the waiting area, or was sent back directly if they chose the apparatus mounted with the non-target temperature. A choice was marked as correct, when the subject chose the

apparatus which held the pad with the target temperature. Set criterion was set as choosing the apparatus mounted with the target temperature in 8/10 trials in four consecutive sessions. The aim of test 1 was to investigate whether the subject was able to retrieve the reward reliably by following the temperature cue of the target temperature.

In case the subject did not reach set criterion or showed a side bias which could not be corrected during test 1 (detailed description of side bias in the section 2.5 Side bias, p. 17), testing was stopped immediately to avoid any wrong associations or formation of habits. The subject continued with three sessions of training 1B, before test 1 was repeated. If the subject did not reach set criterion or displayed a side bias after completing training 1B, test 1 was stopped and the individual continued with test 2.

2.4.4. Test 2

For test 2 the target temperatures were dropped. Instead, one apparatus (the same as used during training 1A and training 1B, except for an altered top of the tower) with two compartments on top of the tower was used (Fig. 1b). Both temperatures were alternately mounted during one session with the order being semi-randomized (same procedure as described in 2.4.2 Training 1B, p. 14). For six subjects (Ke, Ma, Pn, Pl, Sk, Ti) the right compartment was rewarded when the heated-up pad with 40°C was mounted on the apparatus (from the subject's point of view) and the left compartment was rewarded when the cooled down pad with 4°C was mounted on the apparatus (Tab. 1). For the remaining six birds (Di, Je, Pa, Pi, Pu, Sy) it was reversed. The baiting procedure of the compartments of test 2 was identical to test 1.

During test 2 the compartments were covered using metal washer lids (Fig. 1d) which were either heated-up to 40°C or cooled down to 4°C and were covering the compartment of their corresponding temperature. The aim of heating-up/cooling down the metal washer lids was to support the formation of an association between the temperature of the mounted pad and the rewarded compartment by the subject. The temperature of the water inside the buckets which were holding the metal washer lids was measured at the beginning and end of each session with the BOSCH UniversalTemp 3 603 F83 100 infrared thermometer.

During test 2 the subject was allowed to explore the apparatus and interact with both metal washer lids to reveal whether a reward was hidden in the compartment underneath it. The subject was always allowed to retrieve the reward, even if the first choice was the unrewarded compartment. A choice was defined as whenever the subject interacted with one metal washer

lid in a way that revealed the compartment underneath it and hence the presence or absence of the reward. A choice was correct if the subject's first choice was the rewarded compartment. Set criterion was set as choosing the rewarded compartment first in 8/10 trials in two consecutive sessions. The aim of test 2 was to investigate whether the subject is able to reliably choose the rewarded compartment first by following the temperature cue provided by the pad mounted on the apparatus.

During test 2, two exceptions were made regarding the time of testing. The subject Plume (Pl), who was originally part of the afternoon group, started to show a preference for being tested in the test compartment PA (by only entering the test compartment PA, and avoiding the test compartment PO). Since the subject Tai (part of the morning group) was already being tested in the test compartment PA, it was decided to include Plume in the morning group and to conduct the remaining sessions of test 2 of the entire morning group in PA (Je: 6 sessions in PA; Pi: 2 sessions in PA; Pl: 6 sessions in PA; Pn: 6 sessions in PA) to ease the process of testing. After relocating the morning group to the test compartment PA, the subject Kermit, originally also part of the morning group, started to show a preference for the test compartment PO and consequently was switched to the afternoon group which was still tested in PO from session 11 to 15 of test 2. Additionally, as mentioned in the beginning of this section (p. 12), the subject Kermit received the third and fourth session of test 2 on the same day due to an error occurring in session 3 (the compartment which was not assigned to the mounted temperature was baited instead of the usually rewarded compartment). To minimize the formation of incorrect associations session 4 was performed on the same day.

2.5. Side bias

2.5.1. Test 1

During test 1 a subject was considered to show a side bias if the individual approached the same apparatus and hence same side in at least 8/10 trials in one session. In case a side bias was present a bias correction was performed during the next session. For that purpose, the apparatus for which the subject did not show a preference, was mounted with the target temperature and rewarded while the apparatus for which the subject did show a preference was mounted with the non-target temperature (other than that the pads were mounted according to the bias correction, the procedure was identical to test 1 in section 2.4.3 Test 1, p. 15). This procedure was repeated until the subject chose the apparatus, which they did not prefer in the previous session in two consecutive trials or until the tenth trial (one session). In

case the subject approached the apparatus, for which they did not show a preference, in two consecutive trials, the apparatus which was previously preferred was baited in the next trial until the individual, again, chose this apparatus in two consecutive trials, and so forth. If the bias correction was successful, meaning the subject approached the apparatus which they did not prefer in two consecutive trials and then followed the apparatus with the target temperature and reward, test 1 was continued in the next session. Otherwise, the subject underwent three sessions of training 1B or, if already completed, continued with test 2.

2.5.2. Test 2

During test 2 a subject was considered to show a side bias if the same compartment was chosen first in five consecutive trials (also across sessions; for example, if the subject chose the same compartment in trial 8, 9 and 10 of session x and continued to choose this compartment in trial 1 and 2 of session x+1). If this was the case a bias correction was performed by baiting the compartment (and mounting its corresponding temperature on the apparatus) which was not preferred by the subject until the subject chose this compartment first in two consecutive trials or the tenth trial. If the side bias could not be corrected in one session it was continued in the next session, meaning that in such cases the same temperature was mounted in the first and second trial by way of exception. Once the bias correction was successful the order of the temperature and its rewarded compartment was semi-randomized again.

2.6. Analysis

2.6.1. Data analysis

Besides the set criterion, the total number of switching between apparatuses in test 1 and switching between compartments in test 2 before making a choice was observed. A switch from the apparatus with non-target temperature (test 1) or the unrewarded compartment (test 2) to the apparatus with target temperature or the rewarded compartment was interpreted as switching into the correct direction. Switching into the other direction was interpreted as incorrect.

Also, the duration (in seconds) between first touch of the pad mounted with one foot and first touch of the metal washer lid with the beak was coded in test 2 using the VLC media player (version 3.0.11) with the addon Time v3.2.

2.6.2. Statistical analysis

Data preparation and basic analysis was done using Microsoft Excel (Professional Plus 2019). Test statistics was analysed using R (version 4.2.0) (R Core Team, 2022).

The behaviour switching was analysed by comparing the total occurrence of switching with the amounts of switches that were made into the correct direction for each subject. A binomial test was used to test, whether a subject switched significantly more into the correct direction if switching was displayed.

To analyse the duration, Linear mixed models (LMM) and Generalized linear mixed models (GLMM) (Bolker, et al., 2009; Harrison, et al., 2018) were fitted in R (R Core Team, 2022) using the functions "lmer" and "glmer" of the package "lme4" (version 1.1-27.1), respectively (Bates, et al., 2015). Model 1 examined the response variable duration (log-transformed) in test 2, and was fitted with Gaussian error structure and identity link function with "choice" and "session.nr" (session number), as well as their interaction, as key test predictors. The control predictors were "trial.nr" (trial number) and "pad temperature". Model 2 examined the response variable choice (correct or incorrect) in test 2, and was fitted with binomial error structure and logit link function. The key test predictor "session.nr" and the control predictors "trial.nr" and "pad temperature" were included. Bias correction trials were excluded from both models.

In both models, to account for repeated observations of the same individual as well as to avoid pseudo-replication, random intercept effects of individual were included. To avoid overconfident models and to keep Type I error rate at the nominal level of 0,05 (Schielzeth & Forstmeier, 2009; Barr, et al., 2013), all possible identifiable random slopes were included in individual. The covariates "session.nr" and "trial.nr" were z-transformed to ease model convergence and achieve easier interpretable model coefficients (Schielzeth, 2010). After fitting the full model, it was confirmed that none of the model assumptions were violated and model stability was assessed. By visual inspection of qq-plot of residuals and residuals plotted against fitted values, no strong deviations from assumptions of normality and homogeneity of residuals were found after both response variables had been log-transformed (base e). The absence of collinearity was verified by calculating the Variance Inflation Factor (VIF) using the R package "car" (version 3.0-12) (Fox & Weisberg, 2019). Through visual inspection it was assessed whether the best linear unbiased predictors (BLUPs) per level of the random effects were approximately normally distributed (Harrison, et al., 2018). Model stability was assessed with regard to the model estimates, by comparing the estimates from the model including all

data with estimates obtained from models in which the levels of random effects were excluded one at a time (Nieuwenhuis, et al., 2012). All models were of good stability. To avoid "cryptic" multiple testing (Forstmeier & Schielzeth, 2011), each full model with all terms included was compared to a respective null model lacking the key terms of interest (but being identical in random effects part) using the full-null model comparison based on likelihood ratio test. Confidence intervals were calculated for the model estimates by applying the function "bootMer" of the package "lme4", using N=1.000 parametric bootstraps.

3. Results

Overall, eleven birds completed training 1A out of which seven (Di, Ke, Pa, Pi, Pl, Pn, Sk) immediately continued with test 1 (Tab. 2). The bird Mali (Ma) stopped participating after session 2 of training 1A, and therefore was excluded from the experiment. Three out of the seven birds tested in test 1 displayed a side bias (Di: 10/10 trials bias towards left apparatus from subject's point of view; Pn: 10/10 trials bias towards left apparatus; Sk: 9/10 trials bias towards left apparatus) in the very first session of test 1 which could not be corrected in the following bias correction session, and further two showed a side bias during the second session of test 1 (Ke: 9/10 trials bias towards left apparatus; Pl: 8/10 trials bias towards right apparatus). Since side biases were already predominant at early stages of test 1, it was decided that all subjects immediately continued with training 1B as this suggested that the subjects had not associated the target temperature with the reward during training 1A. This also included the remaining birds (Je, Pu, Sy, Ti) still occupied with training 1A and the two birds (Pa, Pi) which have not shown a side bias during test 1. All eleven subjects completed training 1B (Tab. 2).

Table 2: Total number of sessions for each subject (subj.) comprised of training 1A (1A), training 1B (1B), test 1 and test 2. Test 1 is separated into sessions performed after training 1A (left) and sessions performed after training 1B (right).

subj.	total	1A	1B	test 1		test 2
Di	19	3	3	2	1	10
Je	23	4	3	-	1	15
Ke	25	2	3	2	3	15
Ma	2	2		-	-	-
Pa	20	3	3	2	1	10
Pi	17	2	3	1	1	10
Pl	18	2	3	2	1	10
Pn	24	3	3	2	1	15
Pu	7	3	3	-	1	-
Sk	18	2	3	2	1	10
Sy	20	2	3	-	-	15
Ti	20	4	3	-	3	10

Ten subjects were tested in test 1 after completing training 1B. Out of those ten, eight birds showed a side bias during the first session of test 1 (Di: 9/10 trials bias towards left apparatus; Je: 8/10 trials bias towards left apparatus; Pl: 9/10 trials bias towards right apparatus; Pn: 10/10

trials bias towards left apparatus; Pu: 10/10 trials bias towards left apparatus; Sk: 10/10 trials bias towards left apparatus) including the two birds who originally did not show a side bias during the test 1 sessions after training 1A (Pa: 8/10 trials bias towards left apparatus; Pi: 8/10 trials bias towards right apparatus). These subjects were not further tested. The remaining two birds were tested in three sessions of test 1 each, before also displaying a side bias (Ke: 9/10 trials bias towards left apparatus; Ti: 8/10 trials bias towards left apparatus). Since none of the subjects reached set criterion and all of the birds, again, displayed side biases during the early sessions of testing, test 1 was stopped.

The subject Sunny (Sy) started training 1A with a delay (in the middle of May compared to late April for all other subjects) due to time constrictions in the afternoon group. By the time Sunny completed training 1B all birds tested in test 1 had displayed side biases, which lead to the decision that Sunny would not participate in test 1 at all.

Ten subjects were tested in test 2, after the subject Papu (Pu) was excluded due to ignoring the reward on several separate occasions of session 1 test 2. The ten subjects received ten sessions of test 2. None of them reached set criterion (Fig. 4), however, three out of the ten subjects (Je, Ke, Pn) chose the rewarded compartment first in eight out of ten trials during one session (Je: 8/10 choices correct in session 10; Ke: 8/10 choices correct in session 3; Pn: 8/10 choices correct in session 10), thereby reaching parts of the set criterion (Fig. 5). The subject Sunny chose the rewarded compartment first in eight out of ten trials in two non-consecutive sessions (Sy: 8/10 choices correct in session 6; 8/10 choices correct in session 14), hence also reaching parts of the set criterion (Fig. 4). The four birds who reached parts of the set criterion (Je, Ke, Pn, Sy) received five additional sessions of test 2 (15 in total), due to promising development in the course of testing (Fig. 5).
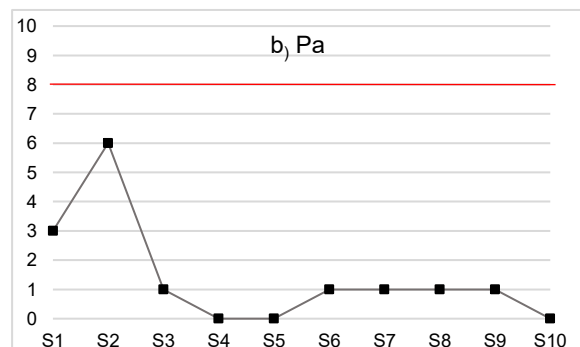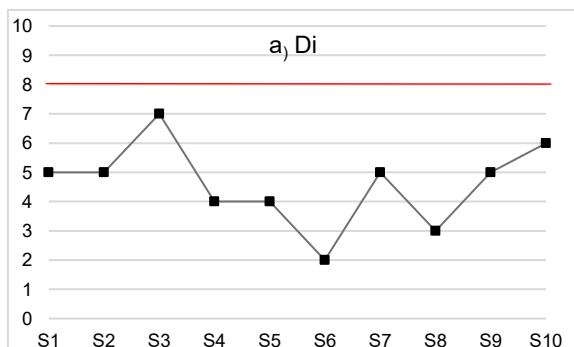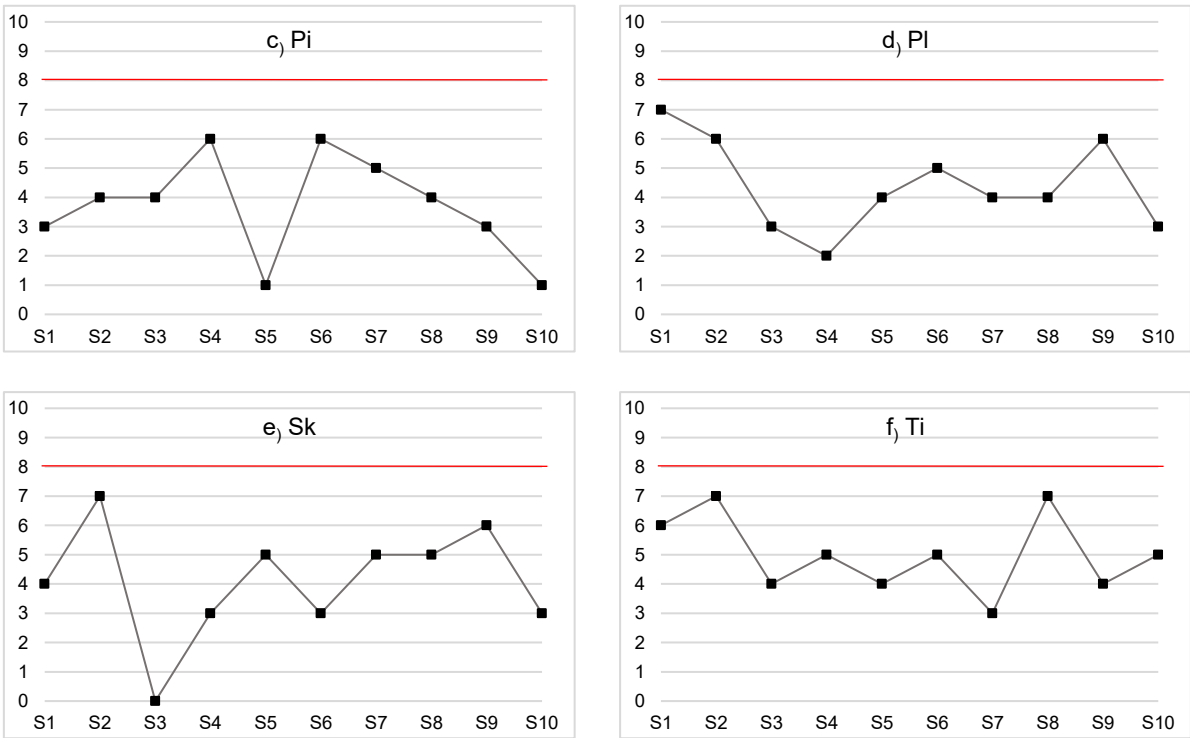
Figure 4: The number of the rewarded compartment chosen first during test 2 for each session (x-axis) for the birds a) Diana (Di), b) Paul (Pa), c) Pick (Pi), d) Plume (Pl), e) Skipper (Sk), and f) Tai (Ti). The y-axis displays the trials. The red line indicates the set criterion. Bias corrections are included.
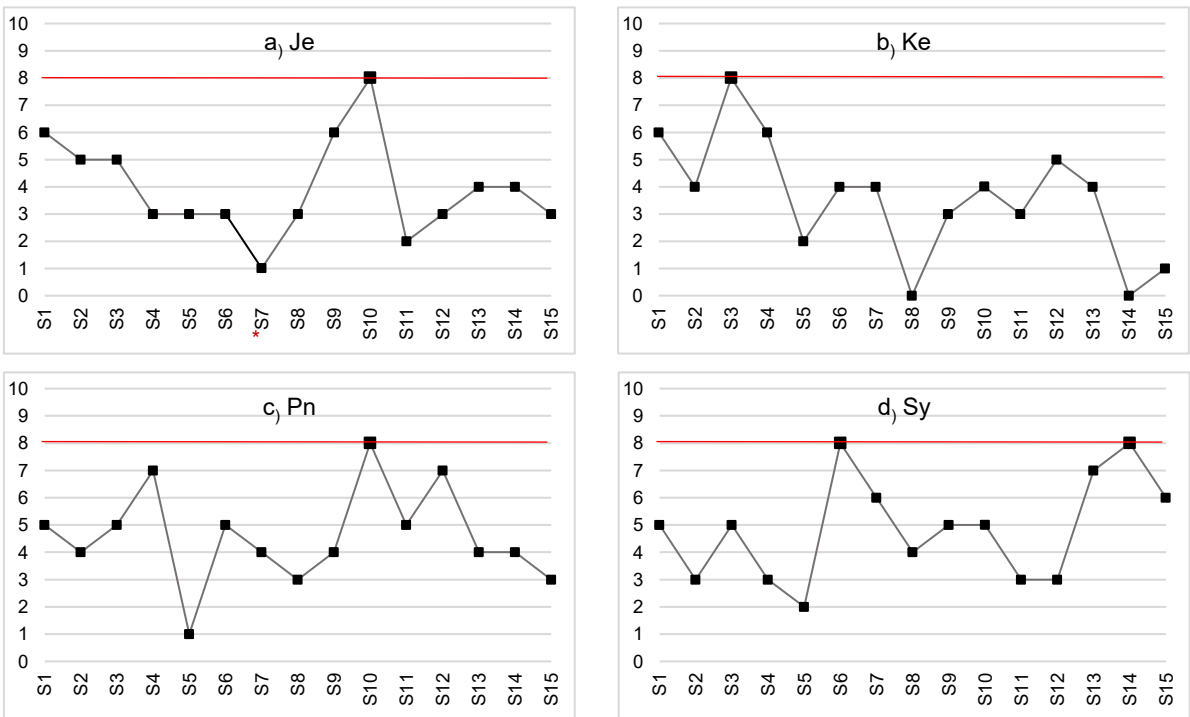
Figure 5: The number of the rewarded compartment chosen first during test 2 for each session (x-axis) for the subjects who reached parts of the set criterion a) Jean-Luc (Je), b) Kermit (Ke), c) Pancake (Pn), and d) Sunny (Sy). The y-axis displays the trials. The red line indicates the set criterion. *S7 of Je was only comprised of nine trials due to an error of the experimenter. Bias corrections are included.

Out of 1199 performed trials in test 2, 511 trials were bias correction trials (Tab. 3). Every subject showed side biases during test 2, however, contrary to test 1, bias corrections were successful. Additionally, subjects showed biases towards both sides, unlike in test 1 where subjects continued to be biased towards only one side. In total 320 bias correction trials were performed to counter a side bias towards the left compartment (from the subject's point of view), and 191 bias correction trials were performed to counter a side bias towards the right compartment (Tab. 3). One exception was the bird Paul (Pa), for whom bias correction was not successful. Paul showed a distinct bias towards the left metal washer lid (from the subject's point of view) starting from session 2 of test 2.

Table 3: The number of bias correction trials (nr. bias corr.) for each subject (subj.) in contrast to all trials (nr. trials) performed during test 2, including bias correction trials to counter a bias towards the left compartment (corr. left bias) and the right compartment (corr. right bias). The total number of trials, bias correction trials, bias correction trials for the left compartment and bias correction trials for the right compartment are indicated in green.

subj.	nr. trials	nr. bias corr.	corr. left bias	corr. right bias
Di	100	30	13	17
Je	149	60	49	11
Ke	150	86	70	16
Pa	100	80	80	-
Pi	100	38	19	19
Pl	100	35	30	5
Pn	150	49	12	37
Sk	100	46	15	31
Sy	150	55	11	44
Ti	100	32	21	11
	1199	511	320	191

3.1. Switching

No switching behaviour was observed during test 1.

During test 2 Jean-Luc (Je) and Plume, both, switched from the rewarded compartment to the unrewarded compartment once in their first session of test 2. Their switching direction was

therefore incorrect. On the one occasion in session 5 where Tai showed switching behaviour, she did so in the correct direction. The subject Sunny showed the behaviour switching thrice during three separate sessions (session 4, 5 and 8). The switching direction was incorrect in session 4 and 5, but correct in session 8 of test 2. Due to too few occasions, the data of the previously named subjects was not included in the statistical analysis.

The subject Kermit displayed a total of 20 switches during test 2, out of which eleven were made into the correct direction (Fig. 6). Pick (Pi) showed a total of nine switches, with five of them made into the correct direction. Both, Kermit ($p=0,324$, binomial test) and Pick ($p=0,500$, binomial test) did not switch into the correct direction significantly more often.
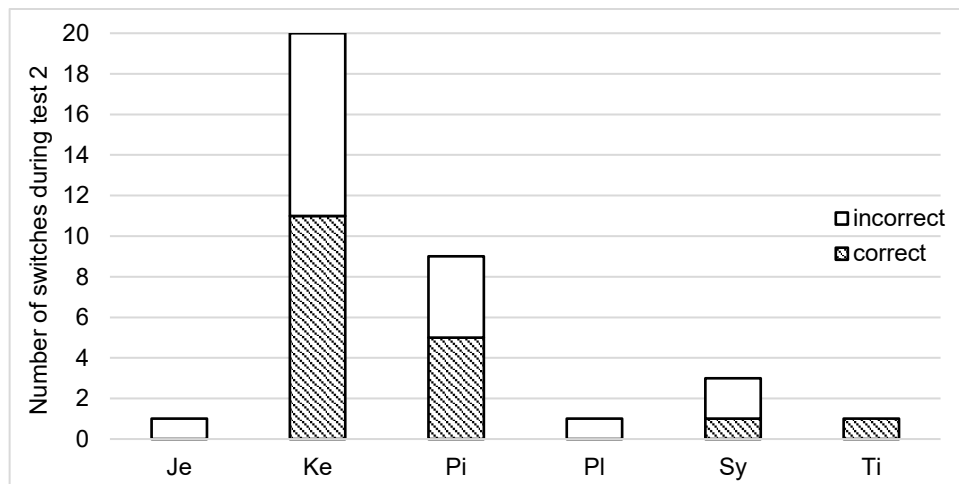
Figure 6: Number of correct and incorrect switches shown by the subjects Jean-Luc (Je), Kermit (Ke), Pick (Pi), Plume (Pl), Sunny (Sy) and Tai (Ti) during test 2.

3.2. Duration

A total of 663 trials from nine subjects (Di: 70 trials, Je: 88 trials, Ke: 63 trials, Pi: 62 trials, Pl: 65 trials, Pn: 100 trials, Sk: 53 trials, Sy: 94 trials, Ti: 68 trials) were included in two models. All bias correction trials were excluded. As the majority of trials of the subject Paul consisted of bias correction trials (Tab. 3), the data of the subject Paul was excluded from the statistical analysis altogether. Additionally, five trials were excluded due to the occurrence of an error (the compartment which was not assigned to the mounted temperature was baited instead of the usually rewarded compartment).

Neither of the two fitted models showed evidence for effects of the test predictors, as indicated by the non-significant difference between full and respective null model (model 1: chisq=7,547, df=6, $P=0,273$; model 2: chisq=3,472, df=2, $P=0,176$). The duration between choosing the

rewarded compartment first (correct choice) and choosing the unrewarded compartment first (incorrect choice), therefore, did not differ significantly (Fig. 7) and the subjects did not choose the correct compartment first significantly more often as the test 2 progressed.
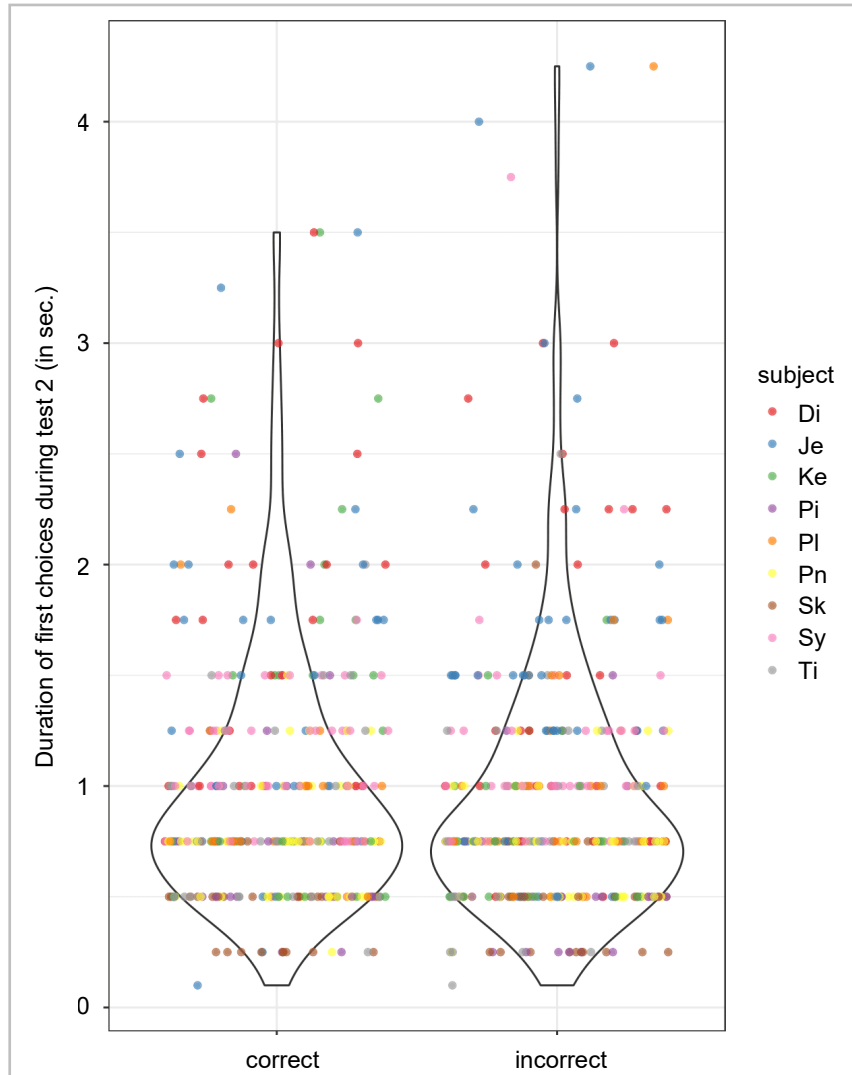
Figure 7: Duration of correct and incorrect first choices in seconds during test 2 of the subjects Diana (Di), Jean-Luc (Je), Kermit (Ke), Pick (Pi), Plume (Pl), Pancake (Pn), Skipper (Sk), Sunny (Sy) and Tai (Ti).

3.3. Ambient and pad temperature

Ambient temperature increased during the entirety of this study (Fig. 8). The average ambient temperature during training 1A was 8,4°C (SD=2,50) in the morning and 9,8°C (SD=4,04) in the afternoon. Compared to this the mean ambient temperatures were already higher during training 1B which was carried out in May (morning: M=16,3°C, SD=2,28; afternoon: M=20,6°C, SD=4,73). The sessions of test 1 immediately carried out after training 1A showed similar

ambient temperatures compared to training 1A (morning: M=9,4°C, SD=2,28; afternoon: M=13,3°C, SD=2,11), while the sessions performed after training 1B at the end of May showed higher ambient temperatures in the morning (M=19,0°C, SD=2,28) and in the afternoon (M=20,2°C, SD=1,40). During test 2 ambient temperatures reached an average of 22,3°C (SD=3,25) in the morning and 26,4°C (SD=4,72) in the afternoon.
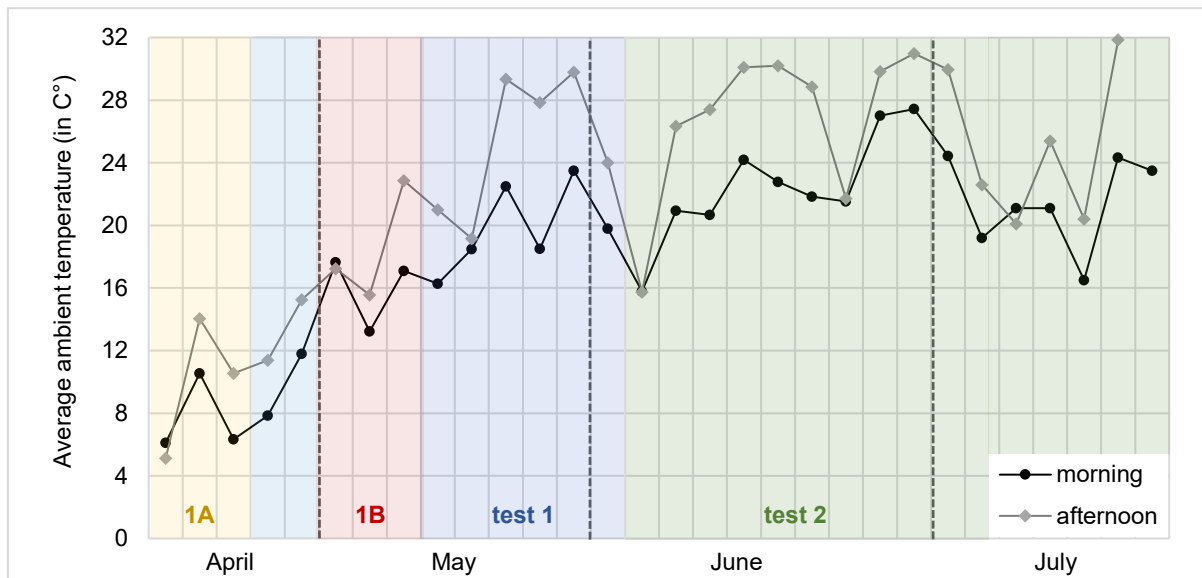
Figure 8: Daily average ambient temperature (in C°) from April to July for the morning (black dot) and the afternoon (grey square) sessions. The different experiment phases are indicated by colour as followed, training 1A (1A) in yellow, training 1B (1B) in red, test 1 in blue and test 2 in green.

Although the ambient temperatures increased, the temperatures of the pads remained within a narrow range throughout almost all of the experiment. During the training steps 1A and 1B the heated-up pad measured an average of 38,6°C (SD=3,43) and 41,5°C (SD=2,10) in the morning and an average of 39,9°C (SD=3,92) and 43,4°C (SD=2,23) in the afternoon, respectively. The mean temperatures of the cooled down pad were also similar across training with -0,9°C (SD=3,62) in the morning and 4,3°C (SD=3,77) in the afternoon for training 1A compared to 3,0°C (SD=4,99) in the morning and 3,6°C (SD=5,29) in the afternoon for training 1B. This was also the case for test 1 after training 1A (morning: M=41,0°C, SD=2,42; afternoon: M=42,4°C, SD=1,96 & morning: M=1,6°C, SD=3,88; afternoon: M=3,6°C, SD=5,43). For test 1 performed after training 1B, the average temperature of the cooled down pad slightly increased for both morning (M=4,2°C, SD=5,54) and afternoon group (M=5,8°C, SD=6,33), in contrast to the average temperature of the heated-up (morning: M=42,5°C, SD=1,87; afternoon: M=42,5°C, SD=1,95) which remained very similar. Also for test 2, the mean

temperature of the heated-up pad (morning: M=42,0°C, SD=2,16; afternoon: M=43,7°C, SD=2,16) was comparable to the ones measured at the beginning of the study. The average temperature of the cooled down pad remained similar for the morning group (M=4,5°C, SD=1,87) as well, while it again increased for the afternoon group (M=7,7°C, SD=5,96). The metal washer lids used in test 2 measured an average of 40,9°C (SD=4,14) and 1,7°C (SD=3,31) in the morning and 41,7°C (SD=3,60) and 1,8°C (SD=3,73) in the afternoon.

4. Discussion

The results support the null hypothesis of test 1 that the temperature did not affect the choice of kea in the two-choice task, and the null hypothesis of test 2 that the temperature did not affect the first choice of kea. Therefore, it was concluded that the subjects tested in this experiment did not follow the temperature cue to reliably retrieve a reward.

None of the subjects reached set criterion (choosing the apparatus mounted with the target temperature in 8/10 trials in four consecutive sessions) in test 1 and none of the subjects reached set criterion (choosing the rewarded compartment first in 8/10 trials in two consecutive sessions) in test 2. The subjects Jean-Luc, Kermit, and Pancake (Pn) have reached parts of the set criterion (choosing the rewarded compartment first in 8/10 trials in one session) in test 2 once. The subject Sunny has reached parts of the set criterion in test 2 twice in two non-consecutive sessions. Further, none of the subjects switched between apparatuses in test 1. The switches between compartments observed in test 2 by the subjects Kermit and Pick were not significantly more often into the correct direction (from the unrewarded compartment towards the rewarded compartment). The subjects also did not choose the rewarded compartment first significantly more often than the unrewarded compartment in test 2 and correct choices were not made significantly faster as the experiment progressed.

A plausible explanation as to why the subjects did not reach set criterion during test 1 could be that they might not have associated the target temperature with the reward during training 1A and training 1B. Without this association, the reward could not be retrieved reliably during test 1 as the subjects did not know which cue predicted its presence or absence. This assumption could also explain why all subjects displayed side biases during test 1, as the strategy of focusing on only one apparatus when unaware of what cue predicts a reward led to success in five out of ten trials. Interestingly, the majority of subjects preferred the left apparatus (from the subject's point of view), which was the apparatus last interacted with by the experimenter before the subjects were allowed to enter the testing area and also the apparatus which was used during training 1A and training 1B. The strategy to first approach the last location of the experimenter when unaware of the location of the reward has been observed in pet dogs (Watson, et al., 2001), and might also be the reason why most kea preferred the left apparatus in this study. Another explanation might be that the apparatuses were not visually identical as intended. It is possible that the subjects were able to distinguish between the apparatuses and preferred the left apparatus as they have experienced it to hold

rewards in training 1A and training 1B. In any case, the display of side biases during test 1 supports the suggestion that the subjects did not understand that the target temperature of the pad mounted on the apparatus predicted the presence of a reward during test 1.

The possible failure to associate the target temperature with the reward might also explain why no subject switched between apparatuses during test 1, as the switch between two apparatuses required the subject to understand that the temperature cue of an apparatus predicted the presence or absence of a reward. A subject had to have associated the target temperature with the reward to understand that when the apparatus approached first held the non-target temperature there was never a reward hidden and that the successful strategy to retrieve the reward could only be to switch to the other apparatus.

The possible failure to associate the temperature with the reward might also be the reason why no subject reached set criterion during test 2. Similar to test 1, in test 2 subjects needed to associate the temperature of the pad mounted on the apparatus with the rewarded compartment to reliably retrieve the reward with their first choice. This might also explain why no subject chose the rewarded compartment first significantly more often as test 2 progressed. This prediction assumed the subject learned that the temperature cue predicted the location of a reward and followed the temperature cue more reliably as they gained more experience, thereby choosing correctly more often in later stages of the experiment. Similarly, the prediction that subjects will make correct choices faster as the study progressed assumed that after the subject associated the temperature cue with the location of the reward, they knew what cue to look for and did so faster as the experiment progresses. As a failed association between temperature cue and rewarded compartment meant that the subject did not know in which compartment the reward was hidden when stepping on the apparatus this would explain why correct and incorrect choices did not differ significantly in their duration.

Yet, the overall performance of subjects was slightly better in test 2 compared to test 1 (reaching parts of set criterion, successful bias correction and occurrence of switches). One reason why results differed could be that the possible confounding factor of the left apparatus which might have influenced the side biases of the majority of subjects during test 1 was removed. As subjects were faced with only one apparatus, they could not focus on which apparatus was approached last by the experimenter or which apparatus was already familiar to them (because it was used during training sessions), thereby giving them the chance to pay attention to other possible cues. Another possibility could be that the added temperature cue

of the metal washer lid in test 2, was the reason for the slight increase of performance. Unlike in test 1, the subjects actively interacted with the temperature cue with their beak through the metal washer lid. Subjects might have noticed that the two metal washer lids differed from one another in some way. Unlikely to the extent that the metal washer lids were heated-up or cooled down and matched the temperature cue of the mounted pad, as none of the subjects reached set criterion. But possibly to such a degree that could have caused them to reconsider the first approached metal washer lid and consequently switch to the other metal washer lid and choose to reveal the compartment underneath it instead, a behaviour which did not occur at all during test 1.

Assuming that the subjects indeed did not associate the temperature cue with the reward and this was the reason why they did not reach set criterion in test 1 and test 2, a possibility as to why the association failed might be due to the lack of salience of the temperature cue. In the current experiment the temperature cue was experienced passively with the feet by stepping on top of the pad during both training phases and test 1. In comparison, when investigating the ability to discriminate weighted objects, Goffin's cockatoos (Lambert, et al., 2021), non-human primates (McCulloch, 1941; Schrauf & Call, 2009), New Caledonian crows and kea (Lambert, et al., 2017), all actively interacted with objects containing the invisible property and, further, had to exchange, lift or insert the target weight during training and, or testing to receive a reward. Similarly, in the studies investigating odour discrimination, birds of prey (Nelson Slater & Hauber, 2017) and the kakapo (Hagelin, 2004) had to manipulate scented objects to retrieve the reward inside. In contrast, the subjects in the current experiment had to manipulate the basic lid covering the reward, which held no relevant cue for the subject during training 1A, training 1B and test 1. Despite the temperature cue being extended to the metal washer lid in test 2, the cue predicting which compartment was rewarded was still experienced passively with the feet. Consequently, the attention of the kea might have focused on the basic lid or metal washer lid, thereby possibly decreasing the salience of the temperature cue of the pad.

A contributor might also have been that the experimenter never visibly manipulated the pad holding the target temperature. Interaction with the pad only occurred outside of visible range of the subject, for example due to opaque, white barriers positioned in front of the apparatus during training 1B, test 1 and test 2. The top of the tower of the apparatus and the basic lid, on the other hand, were visually manipulated during training 1A, possibly (again) making both more salient than the temperature cue provided by the pad.

The pad holding the target temperature being already mounted on the apparatus when the subjects were first introduced to the apparatus during training 1A might have contributed to the lack of salience as well. Since ambient temperatures were inevitably present at any given time of the experiment, the subject might have experienced the temperature of the apparatus as one of many ambient temperatures. Especially since it is not the precise degree Celsius of the environment that is experienced but rather the difference between the ambient and the skin surface temperature (Schmidt-Nielsen, 1997). An individual perceives an ambient temperature decrease of 5°C (from 20°C to 15°C) as cold, due to the skin surface temperature being adjusted to higher ambient temperatures, and consequently the exchange of energy from the skin surface to the environment (Schmidt-Nielsen, 1997). An ambient temperature increase of 5°C (from 10°C to 15°C), on the other hand, is perceived as warm, due to the skin surface temperature being adjusted to lower ambient temperatures and the exchange of energy from the environment to the skin surface (Schmidt-Nielsen, 1997). It has been found that the skin surface temperature of extremities varies strongly dependent on ambient temperatures and can display temperatures within a range of ±2°C of the current ambient temperature, even when ambient temperatures reached as low as 10°C (Bernstein, 1974). As the average ambient temperatures varied across the course of this experiment, while the temperatures of the heated-up and the cooled down pad stayed within a narrow range, the experience of the temperature cue with the feet by the subject might have varied. With the possible lack of consistency of the perception of the temperature cue it might have been difficult to perceive a difference between irrelevant varying ambient temperatures and the varying experience of the relevant pad temperature, thereby possibly decreasing the salience of the pad temperature as well.

It is, however, also possible that kea in general might not be used to actively pay attention to temperature as the passive experience of ambient temperatures is always present throughout their entire life. Issues with salience were also present in a study by Lambert and colleagues (2017), where New Caledonian crows and kea did not associate a visual pattern as cue for their target weight (Lambert, et al., 2017). Once the cue was changed to colour, an ecologically more relevant cue (Møller & Erritzøe, 2010), some subjects reliably associated the visual cue with the invisible property (Lambert, et al., 2017). So, comparable with the visual pattern in the study by Lambert and colleagues (2017), temperature in itself might not be a salient cue, regardless of if the subjects would have interacted with the temperature cue actively or passively.

Another possibility as to why the subjects might not have formed an association between the temperature cue and the reward, besides the salience of the cue, could be that kea are not able to perceive the temperature of the mounted pads with their feet. So far, evidence for thermosensitive receptors reacting to innocuous temperature ranges has only been found in the feathered skin of the wing (Necker & Reiner, 1980) and the beak of pigeons (Necker, 1972; Necker, 1973), as well as the bill of ducks (Gregory, 1973). Although studies have observed that the non-feathered skin of extremities is able to perceive noxious temperature levels (Hau, et al., 2004), up until the present day it is not known if birds are capable of experiencing innocuous temperatures with their feet as well. This might explain why no subject reached set criterion during test 1 and test 2. This could also explain why the subjects showed slightly better performance during test 2 as this might have been the only phase of this experiment where subjects experienced the temperature cue at all and hence possibly also the only phase during this experiment where there was a perceivable difference between certain parts of the apparatus (as one metal washer lid was approximately 4°C and the other 40°C).

4.1. Conclusion and prospect

The current study was the first attempt to investigate whether kea are able to use the invisible property temperature as cue to discriminate in a two-choice task. The subjects did not follow the temperature cue to retrieve the reward reliably in test 1, and the subjects also did not follow the temperature cue to choose the rewarded compartment first reliably in test 2. Therefore, it was concluded that the answer to the research question of this master's thesis was that the kea parrots tested in the current experiment were not using the temperature cue to reliably retrieve a reward.

Future experiments in temperature discrimination should consider the salience of the temperature cue, which might have been an issue in the current experiment. Test setups which require active manipulation of objects holding the temperature cue could be a possibility to increase the salience and are consistent with experiments investigating other invisible properties (McCulloch, 1941; Hagelin, 2004; Schrauf & Call, 2009; Lambert, et al., 2017; Nelson Slater & Hauber, 2017; Lambert, et al., 2021). The beak of kea might be more suitable to manipulate objects containing the temperature cue than the feet as studies have found that the beak of pigeons (Necker, 1972; Necker, 1973) and the bill of ducks (Gregory, 1973) can perceive innocuous temperature ranges. The impact of ambient temperature should be considered as well, as the varying ambient temperatures might have made the experience of

the temperature cue in this experiment inconsistent and possibly indifferent to other ambient temperatures which were inevitably present at any given time. Keeping the ambient temperatures as constant as possible might decrease the possibility that the same temperature cue could be experienced as higher or lower throughout the experiment. When working with target and non-target temperature cues it might be of advantage to present both during training as the subjects might not only associate that the target cue is rewarded but also that non-target cues predict the absence of a reward (see Lambert, et al., 2021 as example). The addition of visual cues during training has also been found to be a prosperous method to train the discrimination between invisible properties and might be helpful during training of future research on temperature discrimination (Lambert, et al., 2021).

5. Abstract

Temperature is a physical property, found to not only be vital for human and non-human animal life but to also influence essential behaviours such as foraging or migration. In the past years, the investigation of invisible properties, characteristics of objects which are not observable with the naked eye, has obtained impressive results showing that animals are able to discriminate between objects through more than just visual cues including discrimination based on weight or odour. No study, so far, has examined whether non-human animals are able to use the invisible property temperature to discriminate objects. The aim of this master's thesis was to investigate whether the kea, a parrot endemic to the mountains of New Zealand and, therefore, ecologically associated with a diversity of environmental temperatures, is able to use temperature as a cue to reliably retrieve a reward. In test 1 ten subjects were confronted with a two-choice task where a reward was hidden in one out of two apparatuses. The reward could be retrieved reliably by following the temperature cue provided by the apparatuses. In test 2 ten subjects were presented with one compartment located on the left side of an apparatus and one compartment located on the right side of the same apparatus. Depending on the temperature cue provided by the apparatus either the left or the right compartment held a hidden reward. None of the subjects reliably followed the temperature cue provided by the apparatus during test 1 and, moreover, none of the kea reliably chose the correct compartment during test 2. It was concluded that the tested kea did not follow temperature cues to reliably retrieve a reward.

Zusammenfassung

In den vergangenen Jahren zeigten beeindruckende Erkenntnisse, dass es einigen Tieren möglich ist, Objekte anhand von nicht sichtbaren Eigenschaften differenzieren zu können, wie beispielsweise Gewicht oder auch Geruch. Zu diesem Zeitpunkt ist noch unklar, ob dies die Eigenschaft Temperatur miteinschließt. Ziel dieser Masterstudie war es, herauszufinden ob Kea Papageien, welche in ihrem natürlichen Umfeld mit verschiedensten Temperaturen konfrontiert sind, dazu in der Lage sind mit Temperatur als einzige Informationsquelle eine Belohnung verlässlich zu entdecken. Dazu wurden den Testsubjekten während Test 1 zwei identische Apparate präsentiert, welche sich nur durch ihre Temperatur unterschieden. Einer von beiden Apparaten enthielt eine versteckte Belohnung, die anhand der Temperatur des Apparates verlässlich entdeckt werden konnte. Weiters, wurden die Kea in einem zweiten Test

mit einem Apparat konfrontiert, welcher zwei Vertiefungen beherbergte. Anhand der Temperatur des Apparates wurde entweder in der linken oder in der rechten Vertiefung eine Belohnung versteckt. Die richtige Vertiefung konnte verlässlich identifiziert werden, wenn die Testsubjekte die Temperatur des Apparates beachteten. Keiner der getesteten Kea war in der Lage die Belohnung verlässlich zu finden, wenn das Testsubjekt mit zwei Apparaten konfrontiert war. Ebenfalls war keiner der Kea dazu in der Lage die richtige Vertiefung anhand der Temperatur des Apparates verlässlich zu identifizieren. Daraus geht hervor, dass die Kea in dieser Masterstudie die Informationsquelle Temperatur nicht in ihrer Entscheidung berücksichtigt haben.

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List of Abbreviations

abbr	abbreviation
asl	above sea level
corr. left bias	bias correction trials to correct for left side bias
corr. right bias	bias correction trials to correct for right side bias
Di	Diana
IR	infrared
Je	Jean-Luc
Ke	Kermit
M	mean
Ma	Mali
nr. bias corr.	number of bias correction trials in test 2
nr. trials	number of trials
PA	*Porticula aurora*; test compartment located to the right
Pa	Paul
Pi	Pick
Pl	Plume
Pn	Pancake
PO	*Porticula occidens*; test compartment located to the left
Pu	Papu
SD	standard deviation
Sk	Skipper
subj	subject
Sy	Sunny
Ti	Tai
1A	training 1A
1B	training 1B
TRP channels	transient receptor potential channels
TRPA	transient receptor potential ankyrin
TRPM	transient receptor potential melastatin
TRPV	transient receptor potential vanilloid

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