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Tactile information improves visual object discrimination in kea, *Nestor notabilis*, and capuchin monkeys, *Sapajus* spp.

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In comparative visual cognition research, the influence of information acquired by nonvisual senses has received little attention. Systematic studies focusing on how the integration of information from sight and touch can affect animal perception are sparse. Here, we investigated whether tactile input improves visual discrimination ability of a bird, the kea, and capuchin monkeys, two species with acute vision, and known for their tendency to handle objects. To this end, we assessed whether, at the attainment of a criterion, accuracy and/or learning speed in the visual modality were enhanced by haptic (i.e. active tactile) exploration of an object. Subjects were trained to select the positive stimulus between two cylinders of the same shape and size, but with different surface structures. In the Sight condition, one pair of cylinders was inserted into transparent Plexiglas tubes. This prevented animals from haptically perceiving the objects' surfaces. In the Sight and Touch condition, one pair of cylinders was not inserted into transparent Plexiglas tubes. This allowed the subjects to perceive the objects' surfaces both visually and haptically. We found that both kea and capuchins (1) showed comparable levels of accuracy at the attainment of the learning criterion in both conditions, but (2) required fewer trials to achieve the criterion in the Sight and Touch condition. Moreover, this study showed that both kea and capuchins can integrate information acquired by the visual and tactile modalities. To our knowledge, this represents the first evidence of visuotactile integration in a bird species. Overall, our findings demonstrate that the acquisition of tactile information while manipulating objects facilitates visual discrimination of objects in two phylogenetically distant species.

In their natural environment organisms receive information through multiple sensory channels. This input is combined into integrated percepts by multisensory systems in which different senses work in parallel (Stein & Meredith, 1993). Object exploration therefore allows the simultaneous acquisition and integration of information gained by different senses. Consequently, at least in species that tend to explore objects by handling them, the information gained from the sense of touch is potentially as important as visual information to interact with surrounding objects.

Interest in the interaction between sight and touch dates back to early research in the study of visual behaviour (e.g. Berkeley, 1709); however, experimental work on visuotactile integration has expanded only in the last few decades and has focused almost exclusively on humans (Gallace & Spence, 2014). Ernst and Banks (2002), in their maximum likelihood estimate model, proposed that humans combine parallel information from visual and haptic senses in a statistically optimal fashion to maximize the precision of the final encoding. Several studies have demonstrated that human subjects trained, either visually or haptically, to identify objects or to recognize categories of objects, when tested in the untrained sensory modality, can transfer knowledge of object identity (e.g. Lacey, Peters, & Sathian, 2007; Lawson, 2009; Norman, Norman, Clayton, Lianekhammy, & Zielke, 2004) and knowledge of object category (Wallraven, Bülthoff, Waterkamp, van Dam, & Gaißert, 2014; Yildirim & Jacobs, 2013) between these two sensory modalities. Particularly, training adults to discriminate shape categories by touch also improved their ability to visually discriminate the same stimuli and vice versa (Wallraven et al., 2014).

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Cross-modal transfer of information between visual and tactile systems has been investigated in a small number of nonhuman species, mainly using matching-to-sample tasks (for a review see Cloke, Jacklin, & Winters, 2015). Davenport and Rogers (1970) provided one of the first demonstrations of cross-modal recognition of stimuli in nonhuman species by testing chimpanzees, *Pan troglodytes*, and orang-utans, *Pongo* sp., in a visuotactile matching-to-sample task. Individuals were required to view a sample object and select one of two visually concealed objects (comparison stimuli) by touch. Subjects trained to match a set of repeatedly presented objects succeeded afterwards in matching (1) novel objects that they had never seen before (Davenport & Rogers, 1970) and (2) objects presented with delay intervals between the presentation of the sample object and the comparison stimuli (Davenport, Rogers, & Russell, 1975). Similar results were shown in monkeys (Cowey & Weiskrantz, 1975; Elliott, 1977; Petrides & Iversen, 1976; Weiskrantz & Cowey, 1975) and more recently in rats, *Rattus* sp. (Reid, Jacklin, & Winters, 2012, 2013; Winters & Reid, 2010). Overall, these studies demonstrated that cross-modal transfer between vision and touch exists in mammalian species, such as chimpanzees, orang-utans, rhesus monkeys, *Macaca mulatta*, capuchin monkeys, *Sapajus apella*, and rats. Aside from studies on mammalian species, cross-modal transfer between vision and touch is mostly unexplored. Moreover, it is still unclear whether, compared to conditions where an animal only has visual cues, visual discrimination ability is enhanced in conditions where an animal can acquire tactile information.

Thus, we considered it important to assess whether species that manipulate edible and nonedible items can use haptic exploration and tactile memories when they need to visually identify objects in the future. This could mean that tactile memory is particularly advantageous since visual discrimination allows individuals to select objects from a distance, before touching them. Moreover, since object discrimination tasks are commonly used in the study of cognitive domains, it is important to evaluate from a methodological point of view whether being able to exploit tactile information might improve object discrimination abilities.

Learning effects, possibly due to tactile information acquired during manipulation, have been reported in two phylogenetically distant vertebrate species: kea, an alpine parrot species (O'Hara, Huber, & Gajdon, 2015), and capuchin monkeys, neotropical primates (Truppa, Carducci, Trapanese, & Hanus, 2015). O'Hara et al. (2015), demonstrated that kea required significantly fewer trials to learn to discriminate objects than their 2D images. Similarly, Truppa et al. (2015) reported that capuchins tested in a visual discrimination task achieved a learning criterion faster when they had the opportunity to manipulate stimuli than when images were presented on a computer screen. Both kea and capuchins have acute vision and a high proclivity to handle and explore objects with their limbs, beaks and mouths (Diamond & Bond, 1999; Fragaszy, Visalberghi, & Fedigan, 2004; O'Hara et al., 2017); thus, it has been hypothesized that both species benefit from tactile information about stimuli. However, the results of O'Hara et al. (2015) and Truppa et al. (2015) could not rule out that these effects were attributable to the types of stimuli that they used in their studies. In fact, aside from the acquisition of tactile information, from a visual perceptual standpoint 2D images carry less visual information than 3D stimuli such as objects. Therefore, to determine whether previous findings on kea and capuchins can be ascribed to additional tactile information, it is important to use the same type of stimuli and control for the opportunity to gain tactile information.

Here we used a two-alternative forced-choice task to assess whether tactile information enhances the visual discrimination capability of kea and capuchin monkeys and affects their performance in an object discrimination task. To our knowledge, this represents the first attempt to evaluate visuotactile integration in a bird species. Individuals were trained to select one of two objects, each of which had a different surface structure. Only one object contained a food reward. Subjects made a choice based on visual cues, and then were allowed to manipulate the chosen object to search for a hidden food item. During the manipulation phase, the opportunity to gain tactile information on the surface of the object was controlled by using objects designed to allow (Sight and Touch condition) or prevent (Sight condition) the acquisition of tactile information that could be used to discriminate between the objects. We hypothesized that both kea and capuchins will take advantage of this tactile information, and thus perform better in the Sight and Touch than the Sight condition. In addition, this study allowed us to evaluate whether these two species benefit from tactile information in a comparable way.

EXPERIMENT ON KEA

Methods

Subjects and housing conditions

We tested eight kea, mountain parrots endemic to New Zealand's South Island (Diamond & Bond, 1999): six males and two females (Table 1). All birds were adults (5–16 years old) born in captivity. They were permanently kept in a well-established group of 22 members housed in a large and environmentally enriched outdoor aviary (52 $\times$ 10 m and 6 m high) at the Haidlhof Research Station, Bad Vöslau, Lower Austria. The aviary was equipped with sand on the ground, hanging branches for perching, two ponds, wooden sleeping and breeding shelters, feeding tables and a variety of enrichment devices that were regularly replaced. Fresh water and bathing opportunities were provided ad libitum. Food was distributed three times daily and consisted of fruits, vegetables, seeds, eggs, meat or cream cheese depending on specific individual diets. The aviary included two breeding compartments and an area that could be divided into seven compartments by sliding wire-mesh doors. Two of these compartments (the experimental

Table 1
Individual data concerning sex, age and performance of kea and capuchins

Subjects	Sex	Age (years)	Learning speed (S&T)	Learning speed (S)	Accuracy score (S&T)	Accuracy score (S)
Kea						
Anu	M	8	112	184	91.67	95.83
John	M	16	184	232	95.83	91.67
Kermit	M	11	112	240	91.67	100.00
Paul	M	5	96	216	100.00	91.67
Pick	M	11	112	192	95.83	95.83
Roku	M	7	112	216	91.67	91.67
Coco	F	8	120	216	87.50	87.50
Sunny	F	8	128	160	91.67	95.83
Capuchins						
Paté	M	25	48	200	87.50	91.67
R. Hood	M	19	64	200	91.67	91.67
Robot	M	21	128	152	95.83	87.50
Sandokan	M	16	120	256	91.67	95.83
Totò	M	6	72	96	91.67	91.67
Vispo	M	16	72	232	100.00	87.50
Carlotta	F	32	112	224	95.83	87.50
Paprica	F	27	32	104	87.50	91.67
Robinia	F	23	104	232	87.50	91.67
Rucola	F	16	104	352	87.50	87.50

M = male, F = female; learning speed = number of trials to achieve the learning criterion; accuracy score = percentage of correct responses at the attainment of the learning criterion; S&T = Sight and Touch condition; S = Sight condition.