their understanding that objects do not change their size while temporarily occluded (size constancy), an ability that develops in children in the first year of life [12,13]. We used the expectancy-violation paradigm, which has been successfully transferred from children to dogs previously (e.g. for a numerosity task [14]). With this approach, a subject’s sensitivity to perceptual changes can be tested. However, it does not necessarily imply complex cognitive processing (e.g. [15]). To rule out possible novelty confounds associated with shaping trials [16], we conducted single-test trials only in a between-subjects design (following [17]).

2. MATERIAL AND METHODS

(a) Subjects and apparatus

Fifty privately owned dogs aged 1–10 years and of various breeds participated in this study—25 males and 25 females (see the electronic supplementary material, table S1, for details). They were shown either an expected or an unexpected event in a between-subjects design. The dogs were assigned randomly to one of the two conditions with the stipulation of a balanced sex ratio in each condition.

The unexpected event consisted of a ball disappearing behind a screen and a ball of different size (but otherwise identical) appearing on the other side. For the expected event, the appearing ball had the same size as the disappearing ball (note that also for this event, two balls were used). The start positions of the two balls were 40 cm to the left of the screen (disappearing ball) and behind the screen (appearing ball, see also electronic supplementary material, figure S1). The end position was behind the screen (disappearing ball) and 40 cm to the right of the screen (appearing ball). The balls used were blue tennis balls with a diameter of 6.5 cm (small) or 10 cm (large). Each dog was followed by one of the following four sequences: (i) small ball disappears, another small ball appears (expected event), (ii) small ball disappears, large ball appears (unexpected event), (iii) large ball disappears, another large ball appears (expected event), and (iv) large ball disappears, small ball appears (unexpected event).

The experimental apparatus (see the electronic supplementary material, figure S1) consisted of a 2 m wooden plank fitted with rails along which the balls were pulled by means of attached transparent nylon strings. The centre part of the plank was occluded by a 93 cm long screen. The strings were operated by the experimenter while hidden behind a barrier placed at the extension of the rail plank. A camera placed at the edge of the barrier on the ground allowed the experimenter to see when the dog was sitting calmly and oriented towards the apparatus. The experiment was recorded with four cameras, one of which was aimed directly at the dog while seated, the remaining ones were placed in three corners of the room.

(b) Procedure

All tests were conducted in the same 5 × 6.4 m large room at the Clever Dog Lab in Vienna. At the beginning of the test, the dog entered the room together with its owner and was allowed to explore the set-up with no balls present for 1 min. Thereafter, the owner was asked to play with the dog for 30 s each with the large and the small ball. The owner and the dog then briefly left the room whereupon the experimenter (Ch.M.) placed the two balls in their respective positions. After the experimenter had taken her position behind the barrier, the dog and the owner re-entered the room, the owner took a seat 2 m in front of the screen, placed the dog between the legs and put on a blindfold. Once the dog was calm and facing the apparatus, the experimenter started the sequence: by means of attached transparent strings, a ball was pulled behind the barrier, whereupon a ball of the same or different size (previously hidden behind the barrier) was pulled out at the other end (see the electronic supplementary material, video clip, for an example).

(c) Analysis

The time that the dog spent looking at the appearing ball was determined from video recordings using frame-by-frame analysis in Sowin2000 (Edwin van Coder v. 10.09 (Andreás Piter, Eotvos Lorand University, Budapest, Hungary)). Looking time was defined as the time spent motionless with the head oriented towards the ball, starting from the time when the ball appeared from behind the screen and ending with the first head movement (upwards, downwards or sideways). We used head direction as a proxy of gaze direction (as in e.g. [14,18]), since pupil direction could not be reliably determined with our set-up. This is because the dogs’ heads had to remain mobile to look first at the disappearing ball and then at the appearing ball and...
thus we could not use close-up recording of the subjects’ eyes. All
the videos were coded by S.D. and Ch.M. (consensus coding).
A random sample (20 of the 50 videos) was additionally coded by
C.A.M. and inter-observer reliability for looking times was high
(Cronbach’s $\alpha = 0.99$, maximum deviation between coders = 2.2 s).

Looking time data were log-transformed and analysed in
R v. 2.10.0 using a general linear model (GLM) with the following
variables included as predictors: experimental condition (expected
versus unexpected), subject sex, size of the appearing ball (large or
small) and play motivation (proportion of time oriented to the ball
in the play session as determined from the video recordings).

3. RESULTS
Overall, looking times were longer when an unex-
pected event was shown than when an expected
event was shown (GLM, $F_{1,45} = 10.3$, $p = 0.002$).
However, this effect was restricted to females and
absent for males (sex $\times$ condition interaction: $F_{1,44} = 5.67$, $p = 0.022$, figure 1). The missing effect for
males was not due to neuter status, as neutered and
intact males looked equally long at the two conditions
(neuter status $\times$ condition interaction: $F_{1,21} = 0.28$,
$p = 0.60$; the electronic supplementary material, table S2). Likewise, no influence of neuter status on looking
time was found for the females (neuter status $\times$ condition
interaction: $F_{1,21} = 0.17$, $p = 0.68$; the electronic sup-
plementary material, table S2). Neither play motivation
nor the size of the appearing ball had an effect on the
dogs’ looking time (table 1).

4. DISCUSSION
Our results show a striking sex difference in a basic
cognitive task: female dogs, but not male dogs,
responded to a size constancy violation with a signifi-
cant increase in looking time. While sex differences
in spatial cognition tasks have been demonstrated in
various rodent and primate species (reviewed in [4]),
where males generally outperform females, our study
to our knowledge provides the first demonstration of
such a sex-specific performance in a physical cognition
task in a non-human mammal. This result is supported
by our reanalysis of the data presented in Rooijakkers
et al. [11], which revealed a similar female advantage
in another object permanence task in dogs, although
not significant, possibly owing to small sample size
($p = 0.079$; see the electronic supplementary material,
table S3 for details). Together, these results suggest
that a sex-biased performance in object permanence
tasks might be a robust phenomenon in dogs.

Three main mechanisms are typically cited as basis
for sex differences in the performance in cognitive
tasks: (i) sex-specific selection pressures in the past,
(ii) sex-specific environmental influences during onto-
geny, and (iii) cognitive differences between sexes as a
by-product of other sex differences. We believe that
the latter explanation is the most likely basis for our results
for the following reasons.

Sex differences in performance in spatial cognition
is typically explained by sex-specific selection pressures
reflecting home range size and lifestyle [4]. In addition,
some of the numerous sex differences found in humans
may be explained by selection pressures that operated
in the past on hunter–gatherer societies [1,2]. In
dogs and their pack-living ancestors, however, life
styles were unlikely to have differed systematically
between the sexes and any division of labour probably
did not extend beyond the task of rearing offspring [19].
Thus, there is no basis for a selection pressure on dog’s
ancestors that could account for the sex-specific
response found here.

Particularly in humans, sex-specific child-rearing
practices may contribute to some cognitive sex differ-
ences [1,2]. This mechanism is unlikely to explain
our results since, unlike in some primates (e.g. [20]),
there is little evidence for such sex-specific experiences
in dogs.

Finally, sex differences in cognitive skills may also
occur as an unselected by-product of other sex differ-
ences, as the brain of young mammals responds to
different levels of sex hormones with sex-specific
differentiation (resulting in an ‘androgenized brain’ in
male mammals [1,2]). Furthermore, even current oes-
trogen and androgen levels in adults have been shown
to influence performance in a variety of cognitive tasks
in humans [1]. Since sex hormones have such far-
reaching effects on mammalian brains, we suggest
that they may cause a variety of basic cognitive differ-
ences between male and female mammals, such as
the differential response in an object permanence
 task presented above. In our specific case, the results
are most probably explained by sex-specific effects on
brain differentiation in early life, rather than current
hormone levels, as later neutering did not change the
performance. Furthermore, the detected sex difference

![Figure 1. Looking time at the appearing ball in the expected and unexpected conditions for males and females separately. Shown are mean ± s.e.m. Filled circles, male; open circles, female.](http://rsbl.royalsocietypublishing.org/Downloaded from http://rsbl.royalsocietypublishing.org/)

Table 1. Factors influencing looking time at the appearing ball. Statistics are given for each factor entered last in a sequential model.

<table>
<thead>
<tr>
<th>explanatory term</th>
<th>$F$-statistic</th>
<th>d.f.</th>
<th>$p$</th>
</tr>
</thead>
<tbody>
<tr>
<td>play motivation</td>
<td>0.39</td>
<td>1,45</td>
<td>0.53</td>
</tr>
<tr>
<td>size of appearing ball</td>
<td>2.35</td>
<td>1,45</td>
<td>0.13</td>
</tr>
<tr>
<td>(large, small)</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>sex (male, female)</td>
<td>0.01</td>
<td>1,45</td>
<td>0.94</td>
</tr>
<tr>
<td>condition (expected, unexpected)</td>
<td>10.4</td>
<td>1,45</td>
<td>0.002</td>
</tr>
<tr>
<td>sex $\times$ condition interaction</td>
<td>5.67</td>
<td>1,44</td>
<td>0.022</td>
</tr>
</tbody>
</table>

*aPer cent of time playing with the balls in the familiarization phase."
is unlikely to be mediated by a simple difference in attention, since overall males did not look less long at the stimuli than females, but may reflect different information-processing strategies between sexes as has been hypothesized for humans [21].

Our study suggests that sex differences in basic cognitive processes may occur widely in mammals, possibly as a consequence of sex-specific differentiation of the brain. Such results will be useful to judge hypotheses put forward to explain differences in cognitive skills between species. In dogs for example, selection pressures associated with domestication are often put forward as an explanation for presence or absence of particular cognitive skills [22,23]. This hypothesis loses support when the ability in question is found only in one of the two sexes. We thus call upon animal cognition researchers to explore possible sex differences in their datasets, rather than being content to report the sex distribution of the sample of subjects studied, and to interpret data on animal cognition with caution when only subjects of one sex were tested or when their sex distribution is strongly biased.

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