

1 **Social information in equine movement gestalts**

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20 **Abstract**

21

22 One model of signal evolution is based on the notion that behaviours become increasingly
23 detached from their original biological functions to obtain a communicative value. Selection may
24 not always favour the evolution of such transitions, for instance, if signalling is costly due to
25 predators usurping signal production. Here, we collected inertial movement sensing data recorded
26 from multiple locations in free ranging horses (*Equus caballus*), which we subjected to a machine
27 learning algorithm to extract kinematic gestalt profiles. This yielded surprisingly rich and multi-
28 layered sets of information. In particular, we were able to discriminate identity, breed, sex and
29 some personality traits from the overall movement patterns of freely moving subjects. Our study
30 suggests that, by attending to movement gestalts, domestic horses, and probably many other
31 group-living animals, have access to rich social information passively but reliably made available
32 by conspecifics, a finding that we discuss in relation to current signal evolution theories.

33

34 Keywords: Animal communication, movement gestalt, signal evolution, phylogenetic
35 ritualization, horse cognition

36 **Introduction**

37

38 Horses are well known for their highly developed perceptual abilities of processing movement
39 patterns (Budiansky 1997; Murphy and Arkins 2007), an ability that may allow them to make
40 inferences about the intentions and motivational states of conspecifics and, after domestication,
41 their human caretakers (Pfungst 1907). We were interested in the origins of these advanced
42 perceptual abilities in domestic horses. We reasoned that their evolution must have emerged from
43 richly available postural information and movement gestalts, naturally produced by conspecifics
44 during daily activities in this highly social species (Laidre and Johnstone 2013). To our
45 knowledge, close to nothing is known about the kind of information naturally available from
46 horses' body movements, despite the likely importance of this channel of information for the
47 evolution of perceptive abilities.

48

49 In our study, we investigated whether and how intrinsic and context-unspecific movement
50 patterns in freely moving domestic horses convey social information. Over evolutionary times,
51 horses have presumably been exposed to high predation pressure, with no real antipredator
52 strategies apart from rapid flight (McGreevy 2004). The ability to recognise and interpret others'
53 movement patterns may be particularly beneficial in such species due to the low signal-to-noise
54 ratio and large variance in information content, a coding strategy that follows subtlety rather than
55 conspicuousness (Laidre and Johnstone 2013). It is also likely that, for similar reasons, the
56 evolution of a rich signal repertoire to coordinate social interactions was equally prevented to
57 avoid attracting predators (Budiansky 1997), especially if alternative modes of information
58 transfer were already effective. One hypothesis therefore is that natural selection has favoured
59 alternative ways of enabling social coordination, bypassing the evolution of dedicated acoustic or

60 visual signals especially at close range, as commonly found in non-human primates (Arbib et al.
61 2008; Budiansky 1997; Laidre and Johnstone 2013). This is not to say that horses do not have a
62 rich communication repertoire, but they may not rely much on this ability when travelling or
63 when exposure to predation is elevated for other reasons.

64
65 We thus focused on information constantly available during natural movements of free-ranging
66 horses. To this end, we recorded movement patterns of freely ranging horses via accelerometers
67 mounted at different locations of their bodies. We temporally aligned the recordings from all
68 sensors and randomly selected brief elements from these recordings for further analyses. This
69 consisted of extracting statistical properties that we then classified using Support Vector
70 Machines (SVMs). Classification was for the class labels identity, sex, breed and two behavioural
71 traits (sensitivity, fearfulness). We first trained a SVM algorithm on a training set consisting of
72 80% of the extracted feature vectors to create a model that best separated the classes (e.g. sex:
73 ‘mare’, ‘stallion’, ‘gelding’). We then used the remaining 20% of the extracted feature vectors as
74 test samples to determine the percentage correct classification of all five categories: ‘identity’
75 (horse 1, horse 2, ... horse n), ‘breed’ (warmblood, coldblood (Edwards 1994)), ‘sex’ (mare,
76 stallion, gelding), fearfulness (four levels) and sensitivity (five levels).

77
78 Accelerometers have already been used in studies of animal behaviour (Gerencser et al. 2013;
79 Graf et al. 2015). To our knowledge, however, previous studies have been based on data from
80 one sensor only, which are unlikely to capture the complex nature of animals’ movement
81 patterns. By positioning six inertial sensors at different body locations, we sought to collect data
82 to determine more complex gestalt profiles, a holistic processing method common in studies of
83 face perception (Dahl et al. 2007; Tanaka and Farah 1991), forensic analysis (Vogelsang et al.

84 2017) and Chinese character recognition (Mo et al. 2015). Accelerometers have also been used in
85 horses to address a range of applied problems relating to health, anomalies and performance, such
86 as to detect lameness (Keegan et al. 2002; McCracken et al. 2012; Starke et al. 2012; Thomsen et
87 al. 2010), analyse rhythmical movements of horse and rider, jumping patters or gait (Burla et al.
88 2014) (Barrey and Galloux 1997), compare hoof ground impact on different surfaces (Ryan et al.
89 2006; Thomason and Peterson 2008) and horse shoes (Dyhre-Poulsen et al. 1994) and evaluate
90 racing abilities (Leleu et al. 2005).

91
92 Here, we were interested in a more basic scientific problem, that is, whether horses could extract
93 social information from observing others' movement patterns. We focussed on a few very basic
94 social parameters, i.e., identity, breed, sex, fearfulness and sensitivity. Horses can individuate
95 conspecifics from their signal production across domains (audio-visual) (Proops and McComb
96 2012; Proops et al. 2009) and are sensitive to others' facial expressions (Wathan and McComb
97 2014; Wathan et al. 2016), but it is not known whether these abilities generalise to movement
98 patterns. While we think it is likely that this is the case, the main purpose of our research is more
99 to demonstrate a principle, which is that naturally available social attributes could be identified
100 through movement patterns.

101

102

103 **Materials and Methods**

104

105 *Subjects*

106 Subjects were 26 healthy horses of warm-blooded and cold-blooded breeds. We used 15 warm-
107 blood breed individuals (2 stallions, age range [years]: M = 13.5, min = 13, max = 14; 6 geldings,

108 age: M = 6.5, min = 5, max = 9; 7 mares, age: M = 7.43, min = 5, max = 17) and 11 cold-blood
109 breed individuals (4 stallions, age: M = 7.5, min = 5, max = 11; 2 geldings, age: M = 8, min = 6,
110 max = 10; 5 mares, age: M = 6.4, min = 2, max = 10). None of the individuals suffered from any
111 orthopaedic or neurological disorders.

112

113 *Data collection*

114 Data were collected at the Swiss National Stud Farm in Avenches, Switzerland, in April and May
115 2016. We used a horse-riding arena of 18 m diameter and sand-dirt footing, providing substantial
116 cushion and traction. In each session we used one horse at the time. Each session contained (1) a
117 preparation phase during which the horse was equipped with custom-made felt-pouches,
118 providing accurate and comparable positioning of the sensors, (2) a habituation phase with the
119 environment and equipment attached in preparation phase, (3) a sensor synchronization phase, (4)
120 a sensor attachment phase, where sensors were placed into the pouches, and (5) a testing phase.

121

122 Preparation phase: Horses were equipped with a bridle, a saddle girth (surcingle), custom-
123 designed bandage boots for the left foreleg and the left hind leg and a bandage at the tail. Prior to
124 the start of the experiment, we mounted two pouches to the bridle, one at the centre point of the
125 noseband ('muzzle') and one on the crownpiece (headpiece) at the horse's 'poll'. We also
126 attached one pouch to the surcingle at the highest point, place right behind the withers ('back'),
127 and one to the dock of the tail wrapped with a bandage centrally placed at a position of 8 cm
128 below the onset of the long, tick tail hair ('tail'). Custom-designed bandage boots were placed at
129 the foreleg on the 'forearm', just above the knee (carpus, carpal bone) and the chestnut, as well as
130 at the hind leg on the 'gaskin' ('second thighs'), above the point of hock (tarsal bones). Pouches
131 were made of felt and of the following dimensions: length = 7 cm, width = 5 cm, height = 3 cm.

132 Using these pouches we could ensure that the data loggers were positioned at fixed anatomical
133 positions. Further, the equipment did not cause any discomfort during locomotion.

134
135 Habituation phase: The horse was free to explore the arena and habituate to the new environment
136 for about 5 to 10 minutes. It also served the purpose to establish initial contact between the horse
137 and the experimenter.

138
139 Sensor synchronisation phase: We first initiated data logging by turning on the individual
140 sensors. We then placed them into a box, aligned according to one predefined dimension, and
141 shook rapidly in each direction for a couple of seconds. This procedure was simultaneously
142 filmed and marked the onset of data recording across loggers to ensure accurate alignment in the
143 data post-processing.

144
145 Sensor attachment phase and experiment initiation: We activated sensors that were placed into
146 the pouches on the horse (Supplementary Figure 1AB). Right after the sensor attachment phase,
147 we initiated the experiment by exercising the horse. Recording samples can be seen in
148 Supplementary Figure 1CD. Since the horses were moving freely without a lunge rein, a strict
149 protocol of behaviour was not possible and not desired. We aimed at natural movement patterns
150 of horses and tolerated character specific behavioural responses. In general, we let the horses
151 walk, trot and canter/gallop for 30 minutes in total, covering both the right as well as the left
152 sides. Commands were given by the handler to encourage the horse during trot and gallop. The
153 amount of time per each gait was not pre-determined, but logically horses tended to walk longer
154 than trot, canter or gallop. Gait frequency, however, did not influence the analysis, since the
155 training and testing samples were selected with equal probabilities from each gait. Additionally,

156 we five-fold cross-validated the analysis procedure, including the selection of training and testing
157 samples.

158

159 *Data analysis*

160 We collected inertial data via custom-made miniature loggers, allowing to record tri-axial
161 accelerometer, gyroscope and magnetometer data. For the analysis we focused solely on the
162 accelerometer output ($\pm 8g$, 16bit, ± 4800 LSB/g (accel sensitivity)). Sensors were factory-
163 calibrated. Inertial sensors were controlled by Arduino Pro Mini 328, 5V/16MHz micro-
164 computers. Data loggers were temporally aligned by manually moving them rapidly in directions
165 of all three axes and simultaneously filming them. In addition, we read out time stamps via a real
166 time clock. We read out data at 128Hz onto a SD card and later downloaded data files onto a PC
167 for analysis.

168

169 Data pre-processing and feature extraction: We first applied feature scaling to the raw values of
170 each sensor and each axis by bringing all values into a range of [0,1]. We then aligned these
171 values and merged them to one file per individual, representing the unity-based normalized
172 acceleration values of all sensors and all axes as a function of time. For each individual we
173 extracted 100 non-overlapping segments at random points in time. Each segment consisted of 256
174 samples, equivalent to 1 second. For each of these segments and on all axes (a_x , a_y , a_z , a_x/a_z , $|a|$)
175 we extracted statistical features as follows: (1) standard deviation, (2) mean, (3) min, (4) max, (5)
176 root mean square (rms), (6) auto-correlation: height of main, height and position of second peak,
177 (7) spectral peak features: height and position of first six peaks, (8) spectral power features:
178 power of five adjacent frequency bands (edges: .5, 1.5, 5, 10, 20 kHz), (9) skewness, and (10)
179 peaks: number, std(width), std(prominence). Importantly, the a_x/a_z component reflected the

180 tangent of the cranio-caudal direction relative to the ground. The acceleration magnitude ($|a|$) was
181 equal to the $\sqrt{x^2 + y^2 + z^2}$. In total, we calculated 105 features for each sensor, hence 630
182 features for each one-second segment. All features were normalized to a range of [0 to 1]
183 (Supplementary Figure 1E). A similar approach on feature extraction has been used in
184 quantifying movement of freely ranging dogs (Gerencser et al. 2013).

185
186 Classification algorithm: We used Support Vector Machine (SVM), a supervised learning
187 algorithm, to classify these segments. A SVM classification routine encompasses a training
188 phase, during which a model will be derived that best separates samples of two classes, and a
189 testing phase, during which the model will be evaluated by determining the performance on novel
190 samples. We used the libsvm toolbox (Chang and Lin 2011) for implementing the SVM
191 algorithm. Inputs to the SVM algorithm were predetermined 630-element feature vectors, as
192 described above, split into 80% (160) training and 20% (40) testing samples. In the SVM
193 algorithm we used a radial basis function (RBF) Kernel. The two unknown parameters, the soft
194 margin (C) and the kernel parameter (gamma) (Cortes and Vapnik 1995), were determined in a
195 five-fold cross-validation procedure on dedicated smaller numbers of samples, trading
196 classification errors penalty for stability and thus leading to a higher degree of generalization
197 rather than over-optimization. C and gamma were determined individually for each comparison.
198 We then fed all training samples as well as their labels, the correct classification outputs, into the
199 SVM algorithm to generate the best fitting model. All testing samples, i.e., unknown, novel
200 inputs, were then fed into the model, predictions obtained by the model and compared to the
201 desired output.

202

203 We applied this principle to the following class labels: ‘identity’ (‘horse 1’, ‘horse 2’,... horse n),
204 ‘breed’ (‘cold-blooded’, ‘warm-blooded’), ‘sex’ (‘mare’, ‘stallion’, ‘gelding’), ‘fearfulness’
205 (three classes of varying degrees, see below) and ‘sensitivity’ (four classes of varying degrees,
206 see below).

207
208 We obtained performance scores for all attribute labels as described above in a pairwise fashion,
209 i.e. always two class labels (Fig. 1). Figure 1 shows the performance scores as percentages of
210 prediction. For example, assuming the actual outcome (y-axis) was ‘warmblood’ (WB) as the
211 type of horse ‘breed’ (Fig. 1C), then 80.5% were correctly predicted (x-axis) and 19.5% were
212 incorrectly predicted. Importantly, for classes with more than two labels, the chance level was
213 still 50% due to the pairwise comparisons of SVM.

214
215 Feature selection: It is important to note that classification performance is generally influenced by
216 the number of feature dimensions. Therefore, in a second step, we aimed at optimizing the model
217 by reducing the feature dimensions to avoid overfitting to irrelevant dimensions (noise), save
218 storage space and reduce computation time. We therefore implemented two methods: (1) Feature
219 selection using a filter approach: with this approach we relied on the statistical features of our
220 data by calculating *t*-tests for each feature between the samples of the two classes of interest
221 (Jafari and Azuaje 2006; Liu et al. 2004). This procedure resulted in *p*-value for each feature
222 dimension reflecting the effectiveness of features for those two classes. (2) Sequential feature
223 selection: on top of a selected subset of features individual feature dimensions was added
224 (forward search) until there was no further improvement or a maximum of 20 features was
225 reached (Li et al. 2004; Resson et al. 2005). We use a hybrid-method by combining these two
226 approaches by first selecting statistically important feature dimensions and then sequentially

227 searching for the best combinations of features (Fig 2A). In this training period, we also applied a
228 five-fold cross-validation routine. Figure 2A shows the means of all features (grey dots) and the
229 20 most discriminative features (blue circles) of two horses (ID1 vs ID2). As can be seen, the
230 features selected deviated strongly from the diagonal line, indicating different expressions of
231 those particular features for the given classes.

232
233 Control condition: We also calculated a performance baseline, which was determined by random
234 labelling of training samples, while maintaining the remaining processing routine as described
235 above. Reported in Figure 1 are the performance scores after the hybrid-method for feature
236 selection. We further calculated the probability of statistical feature types among the selected
237 features as a function of attribute ('identity', 'breed', 'sex', 'sensitivity', 'fearfulness') and
238 anatomical sensor position ('forearm', 'gaskin', 'back', 'tail', 'muzzle', 'poll'). To calculate
239 whether correct classification occurred more often than incorrect classification, we used χ^2 -tests
240 of independence. We therefore compared the correct classification (observed values, see
241 diagonals in Fig. 1 A,C,E,G,I) with an expected outcome of 50%. We calculated proportional
242 contribution of features for each attribute and each anatomical location (Fig. 3A-E) and used a
243 hierarchical clustering algorithm to illustrate the similarity of gestalt profiles (Fig. 3F).

244
245 Statistical tests: We used Chi-Square tests of independence to evaluate whether there was a
246 significant association between the correct and incorrect classifications for all attributes.

247

248 *Personality traits*

249 Aside from the intrinsic information ('identity', 'breed', 'sex') we included two personality traits
250 ('sensitivity', 'fearfulness') in our analysis. These traits were measured in separate experimental
251 sessions and are parts of the Complete Personality Tests (CPT) (Lansade et al. 2016).

252
253 *Tactile sensitivity:* The tactile sensitivity test describes the degree to which an individual
254 responds to tactile stimulation, reflecting a basic sensory disposition to environmental
255 stimulation. The underlying assumption is that responsiveness toward tactile stimulation
256 generalizes to other sensory domains. The testing procedure is as follows: The horse was held
257 immobile in hand. Filaments (Frey nylon filaments of 0.008g, 0.02g, 1g and 300g, Stoelting, IL
258 USA) were individually perpendicularly applied to the base of the withers. Constant pressure was
259 applied to the filament until it bent. The procedure was repeated for all filaments alternating the
260 left and right sides of the withers. A natural response of the horse is to shiver the platysma
261 muscle to a perceived tactile stimulation. The response ratio describes the tactile sensitivity.

262
263 *Fearfulness:* A critical aspect of this test is the suddenness of a stimulus occurring. The horse was
264 held in hand via a long rein, while a second person was positioned at given distance (first trial at
265 5m, second trial at 2m) in front of the horse. The second person then rapidly opened and closed a
266 black umbrella and put it down on the floor in front of herself. The evasion away from the
267 umbrella was quantified via video recordings and averaged across trials (2 and 5m distances).

268

269

270 **Results**

271

272 Our model was able to classify ‘identity’ at 95.8% (Fig. 1A), ‘breed’ at 82.9% (Fig. 1C) and ‘sex’
273 at 86.9% (Fig. 1E) correct classifications. The two personality traits ‘fearfulness’ and ‘sensitivity’
274 were classified correctly at 81.2% (Fig. 1G) and 86.5% (Fig. 1I), respectively. We contrasted
275 these classification results with a randomly expected outcome (Control condition). The randomly
276 expected outcome was 50% correct classification due to SVM’s pairwise comparisons. The actual
277 performance of the control model were as follows: ‘identity’: 49.8% (Fig. 1B); ‘breed’: 52.6%
278 (Fig. 1D); ‘sex’: 50.8% (Fig. 1F); ‘fearfulness’: 46.3% (Fig. 1H); ‘sensitivity’: 51.4% (Fig. 1J).
279 We found that, in all test runs, occurrences of correct classifications (i.e. when the predicted
280 outcome matched the actual outcome) were significantly higher than incorrect classifications (i.e.
281 when the predicted outcome did not match the actual outcome) (Table 1). This was not the case
282 in the control conditions, as expected, ruling out idiosyncratic response patterns in the test runs
283 not due to the attributes under investigation. The largest portion of misclassification was in the
284 attribute ‘sex’, where geldings and mares were mutually misclassified more often than expected.
285 We found a difference in geldings being more often misclassified as mares (11.9%), and vice-
286 versa (10.8%), compared to the expected level of misclassification (7.85%, 7.65%): (χ^2 (1, N =
287 100) = 13, p = 0.001).

288

289 *How is information conveyed?*

290 To determine which of the extracted features accounted for the high classification rates, we
291 analysed the outcome of the feature selection procedure prior to classification (see Methods and
292 Fig. 2A, B). We were interested in the explanatory power of the statistical features with regard to
293 attributes and anatomical locations (Fig. 3D). Overall, the means of the signal elements in any of
294 the three axes as well as the spectral peaks and spectral power played the most crucial roles (Fig.
295 3B, C), as visualized by the size of the circles. The importance of these features, however,

296 slightly varied depending on the attribute (Fig. 3A, B). While ‘identity’ could be explained to a
297 large degree by variances in the means of the signal elements, ‘sex’, ‘fearfulness’ and
298 ‘sensitivity’ could be best explained by a combination of spectral features and statistical means
299 (Fig. 3A, B). The attribute ‘breed’ was best described via contributions of the means, spectral
300 features and the statistical mean of the squares of the signal elements (RMS). Importantly, for
301 each attribute a combination of distinct locations (sensors) contributed to correct predictions (Fig.
302 3A, D). While ‘identity’ could be best accounted for by a combination of sensors at all
303 anatomical locations, ‘breed’ and ‘sex’ were predominantly described by the poll and the tail in
304 combination with other locations of minor importance. The personality trait ‘fearfulness’ was
305 best detectable via the gaskin, the poll and the tail, depicting a different configuration of
306 anatomical locations than ‘sensitivity’, which mainly differentiated via the sensors at the head
307 (poll and muzzle), the back and the tail. The importance of the sensory configuration is further
308 highlighted in Figure 4A.

309
310 We further compared the resulting gestalt profiles by calculating a hierarchical cluster tree (Fig.
311 3F). It turned out that ‘breed’ and ‘fearfulness’ built one pair of close similarity and ‘sex’ and
312 ‘sensitivity’ built another. ‘Identity’, however, due to a more equal contribution of all anatomical
313 location, fell into its own class. In the next step we determined the degree to which each of the
314 anatomical location differed from a random allocation of features to the six locations (Fig. 3E). In
315 other words, do contributions of individual anatomical locations to the classification outcome
316 deviate from a random distribution of features where all locations contribute equally? We found
317 that all (but two) locations were significantly different from the random distribution at a
318 significance level of 5% (Fig. 3E: two standard deviations of random distribution shown in grey).
319 Importantly, each attribute showed a set of locations that was over-represented (above the grey

320 vertical bars in Fig. 3E), hence contributing positively to the classification outcome, and another
321 set that was under-represented (below the grey vertical bars in Fig. 3E), hence being an unreliable
322 source of information for that attribute. Figure 4B shows the under- (green circles) and over-
323 represented locations (red circles) visually.

324

325

326 **Discussion**

327

328 One evolutionary model of communication is that both fixed cues and flexible signals originate
329 from more basic, biologically functional processes by a process of ritualization. An interesting
330 problem therefore is under what conditions such processes can evolve into communication
331 signals and how this happens. One way by which selection favours the evolution of signals is by
332 increasing the contrast, amplitude, or conspicuousness of an already existing behaviour.

333

334 In this study, we were interested whether movement gestalts of free-ranging horses contained
335 social information potentially relevant for others, which would provide the breeding ground for
336 signal evolution. Our learning algorithm classified signaller attributes from kinematic movement
337 patterns with high accuracy. Information about identity was most accurate, resulting in correct
338 classification of 96%, while breed, sex, and personality traits ranged somewhere between 80 to
339 90% correct classification, significantly higher than if randomly assigned to training samples.

340 Our results thus highlight the information power of movement patterns, irrespective of gait,
341 context or other external factors. The level at which the model derived information of complex
342 attributes was intriguingly accurate, highlighting the advantage of machine learning approaches
343 over classic ethological methodology.

344
345 Another main finding in our study was that, by combining the results of distinct anatomical
346 locations, classification was especially successful. For instance, the attributes ‘sex’, ‘breed’,
347 ‘sensitivity’ and ‘fearfulness’ was best discriminated by head movements (determined at the poll
348 and muzzle) in combination with movements of the tail. For identity, the most successful
349 combination was between movements of the gaskin, tail and back, further highlighting the gestalt
350 nature of feature discrimination. Interestingly, misclassifications in ‘sex’ resulted in mares and
351 geldings being often confused, reflecting the effects of castration of stallions, which tends to alter
352 their behaviour towards a quieter, more easily-controllable, well-behaving and tractable
353 “working” horse (Kiley 1976).

354
355 *Is movement perceived as information?*

356 Our analyses have shown that natural movement patterns can contain rich sets of information, but
357 are they also processed by recipients? Experimental testing on the discrimination abilities of the
358 different attributes would be a considerable challenge.

359 The following theoretical arguments, however, suggest that horses are expected to access
360 information generated by movement patterns. First, movement patterns are readily available in
361 this species, regardless of context. Information can thus be produced at virtually no extra costs,
362 much in contrast to ritualised signals, and this may also provide less of a demand on receiver
363 cognition. Second, feral horses are adapted to open grassland habitats, where the visual domain
364 plays an important role, in contrast to visually dense forest habitats. Indeed, the acoustic
365 repertoire of horses is relatively small, consisting of mainly four types of vocalizations (whinny,
366 nicker, squeal, and roar) (Kiley 1972). Visual cues, such as facial expressions (Wathan and
367 McComb 2014; Wathan et al. 2016), are visible only in close proximity, suggesting that

368 movement patterns may be more efficient for information transfer at large distances. In contrast
369 to other ungulates, social dominance in horses is not determined by size or weight (Duncan 1992;
370 Feh 1990), but by social factors, such as age and migration status (Monard and Duncan 1996).
371 Overall, we find it plausible that movement patterns play a role in horse communication, a
372 hypothesis that has already been put forward by early work on animal cognition (Pfungst 1907).

373
374 In our study, we assumed that, similarly to face discrimination (Dahl et al. 2016; Fific and
375 Townsend 2010), the neural machinery of kinematic gestalt processing in mammals processes
376 limb movements in a non-linear space by which the relevant features are extracted from a high-
377 dimensional space and then processed in a parallel coactive fashion. This processing is a
378 reasonable assumption to support the demand for efficient neural processing that can potentially
379 allow for rapid decision making. One way to optimise the representational embedding of
380 kinematic features is by reducing high dimensionality to a subspace that represents most
381 kinematic variance. Reducing dimensionality, therefore, reduces processing time and storage
382 space. To simulate this biologically plausible process, we optimised the feature selection process
383 using a sequential feature selection approach, selecting the twenty features that sequentially add
384 most of increment in correct prediction.

385
386 *Social information from movement*

387 Our choice of social attributes (identity, sex, breed and personality factors) was practically and
388 not theoretically motivated, mainly due to ease of accessibility. Our goal was to demonstrate the
389 principles of a new methodology, but we predict that social information contained in movement
390 patterns goes beyond the small number of attributes we chose in this study. Nevertheless, the
391 current attributes may have relevance in wild horses in the following ways. First, attributes such

392 as identity, sex or breed (representative of morphological features) may be important in rapid
393 assessments by stallions in their attempts to monopolise a group of mares. While mares tend to
394 lead social groups to resources, stallions tend to follow in the rear (Briard et al. 2017), suggesting
395 that rapid identification at larger distances is essential for them. Similar arguments could be made
396 for mares, if there is a danger of infanticide by out-group males. Further, personality traits, such
397 as fearfulness, may be important in rapid assessments of unfamiliar rivals or sexual partners
398 (Linklater et al. 2000; McDonnell and Haviland 1995; Miller and Denniston 1979)

399

400 *A quantitative approach to ethology*

401 Ethology aims to address biological questions about animal behaviour in natural conditions. The
402 classic methodological approach has always been to first determine a species' behavioural
403 repertoire, the 'ethogram', in order to code behavioural elements according to different sampling
404 regimes (Altmann 1974). Although this has been an extremely successful and productive
405 approach, its main weakness is that behavioural elements are subjectively coded by human
406 observers, rather than by objective measurements. The difficulties of this approach is well
407 illustrated, for example, in ape gestural studies where observational studies on gesture repertoires
408 of wild chimpanzees can generate wildly different results (N = 66 gestures (Hobaiter and Byrne
409 2011; Hobaiter and Byrne 2014); N = 30 gestures (Roberts et al. 2012)), even if collected from
410 the same community. Thus, the quest to standardize behavioural repertoires is a challenging task
411 and recording the full behavioural repertoire of a species via traditional ethograms is nearly
412 impossible, and even partial descriptions of repertoires are extremely time-consuming and highly
413 subjective.

414

415 The advent of inertial sensor techniques in digital information processing provides a new and
416 powerful tool to record continuous movement data from freely moving animals in their natural
417 environment and, therefore, opens the doors to novel and more objective sampling regimes.
418 Inertial measurement units (IMU), routinely used in air- and spacecraft, log body-specific forces
419 at high frequencies locally on a memory device (logger). Data logging via IMUs is an automated
420 and entirely objective process, allowing measurements of animals in the wild, out-of-sight and in
421 difficult terrain. With the novel technology, however, novel challenges rise, such as finding the
422 right means of handling big data and algorithms for an automated classification of behaviour.
423 Hence, new research routines ought to integrate methods of behavioural animal science and
424 machine learning. Along the line of previous research programs (Gerencser et al. 2013; Graf et al.
425 2015), we here present one way of combining the two fields.

426

427 *Conclusion*

428 In this study we showed that movement patterns of freely moving animals contain a large amount
429 of socially relevant information, which potentially can be accessed by conspecifics. Information
430 transfer via movement patterns therefore follows a principle of subtlety rather than
431 conspicuousness, a principle of information transfer in animals which is largely unexplored.
432 Further, our study offers a new tool to investigate behavioural patterns in a wide range of
433 animals. Bio-logging via inertial sensor techniques replace video camera recording and its
434 extensive analysis procedure. An expert system, as presented here, helps automating ethological
435 investigations in that it classifies movement patterns of freely moving animals into meaningful
436 classes. Future directions might incorporate unsupervised learning algorithms, implying that no
437 a-priori assumption about attribute labels is required.

438

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444 Author contributions: CDD: study design, data collection, analysis and interpretation, writing
445 article, provision of necessary tools; CW: data collection; KZ: provision of necessary tools and
446 resources, writing article; IB: provision of necessary tools and resources.

447

448 Compliance with ethical standards

449 Conflict of interest: All authors declare that they have no conflict of interest. The authors have no
450 affiliations with or involvement in any organization or entity with any financial interest, or non-
451 financial interest in the subject matter or materials discussed in this manuscript.

452 Ethical approval: All applicable international, national, and/or institutional guidelines for the care
453 and use of animals were followed, i.e., the Swiss law on animal protection and welfare. This
454 study was approved by the Swiss Federal Veterinary Office (approval number VD-3103).

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458

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580

581 **Figure captions**

582

583 Figure 1. Confusion matrices of classification outcome. Matrices A, C, E, G, and I show the
584 actual test conditions for the attributes ‘identity’, ‘breed’, ‘sex’, ‘fearfulness’ and ‘sensitivity’.
585 Matrices B, D, F, H and J show the control conditions. Each confusion matrix shows the ‘actual’
586 outcome (y-axis) against the ‘predicted’ outcome (x-axis). Percentage correct classifications are
587 indicated on the diagonal line in each confusion matrix. Colour-codes indicate the percentage
588 correct classification with 100% in black and 0% in white.

589

590 Figure 2. Feature evaluation. A. Feature selection for classification of ID1 vs ID2. Grey dots
591 illustrate the mean values of features for ID1 (x-axis) vs ID2 (y-axis). The blue circles mark the
592 features selected by our hybrid feature selection procedure. B. Feature selection for classification
593 of ‘Mare’ vs ‘Stallion’.

594

595 Figure 3. Explanatory power of features and locations. A. Feature probabilities for each
596 anatomical location (x-axis) and attribute (y-axis). Grey vertical lines separate the six locations
597 (sensors). Each separation contains 105 features (see Methods). Probabilities are only implied.
598 Black vertical lines indicate the cumulative probabilities across attributes. B. Probability of
599 feature types (x-axis) by attributes (y-axis). Large circles indicate high probabilities, smaller
600 circles low probability. C. Probability of feature types (x-axis) by anatomical locations (y-axis).
601 D. Average feature probability per anatomical locations (x-axis) and attributes (y-axis). E.
602 Contribution (feature probability) for each attribute (as in D) compared with random distribution
603 (grey bars). Each bar shows the range of two standard deviations (95.4% of the variance). F.

604 Similarity of gestalt profiles. The heights of the inversely u-shaped elements in the tree indicate
605 the Euclidean distance between the two profiles being connected.

606

607 Figure 4. Gestalt profiles. A. The relative contribution of sensors at given anatomical locations is
608 represented in the sizes of the circles, with increasing size indicating greater relative importance.
609 Shown are the locations that together explain more or equal than 70% of the cumulative
610 contribution of locations, starting with the location with the largest contribution. B. Each attribute
611 is described by the locations (circles) that contributed more (red) or less (green) than expected by
612 an equal contribution of all locations. Blue circles show the locations that fell into the expected
613 range of equal contribution.

614 **Tables**

615

616 Table 1:

	χ -Test	p-val Test	χ -Control	p-val Control	DF
Identity	7083.9	0.001	4.43	1	25
Breed	125.58	0.001	0.71	0.40	1
Sex	286.31	0.001	0.20	0.90	2
Fearfulness	207.39	0.001	2.93	0.23	2
Sensitivity	382.3	0.001	1.83	0.61	3

617

618

619

620 **Table caption**

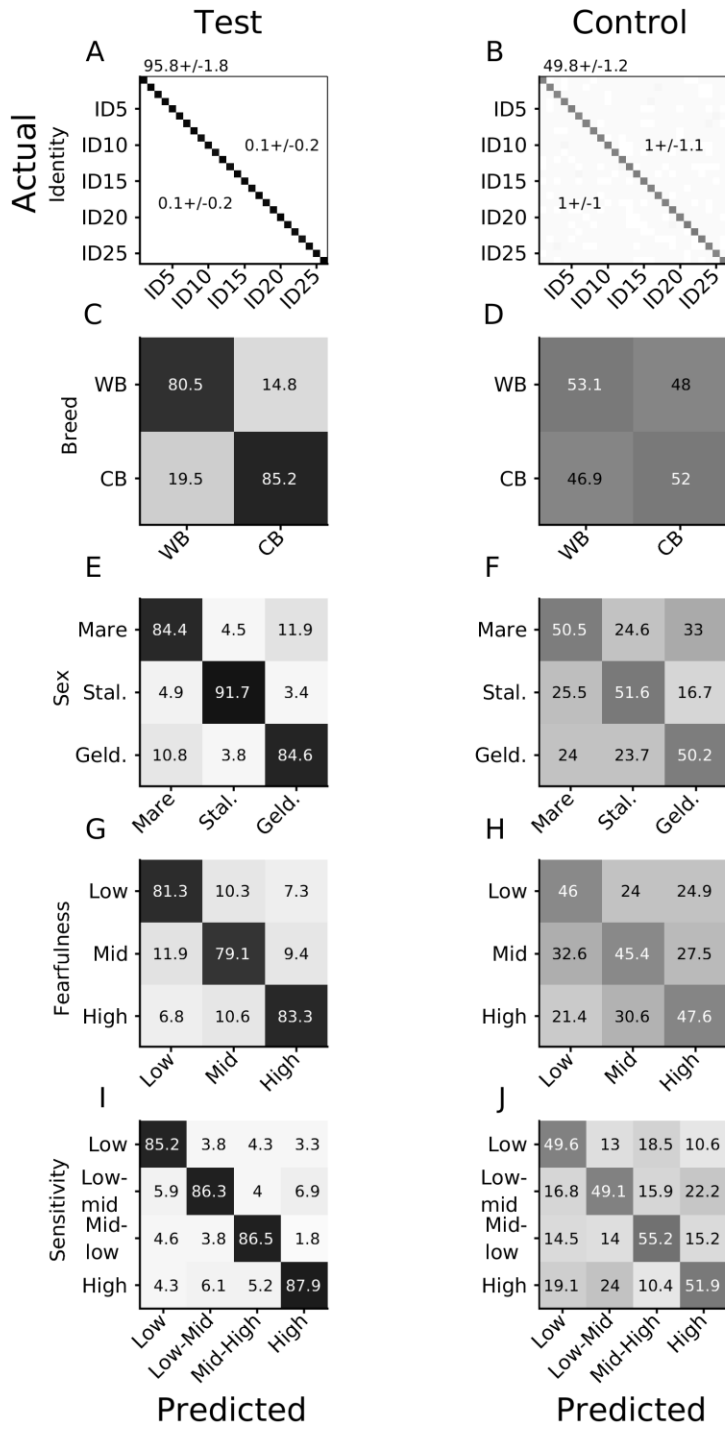
621

622 Table 1: Statistical values for all attributes evaluated using Chi-Square tests of independence.

623

624 **Figures**

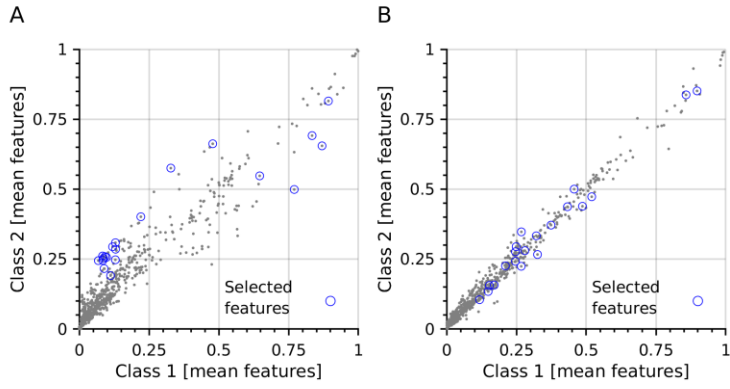
625 **Figure1**



626

627

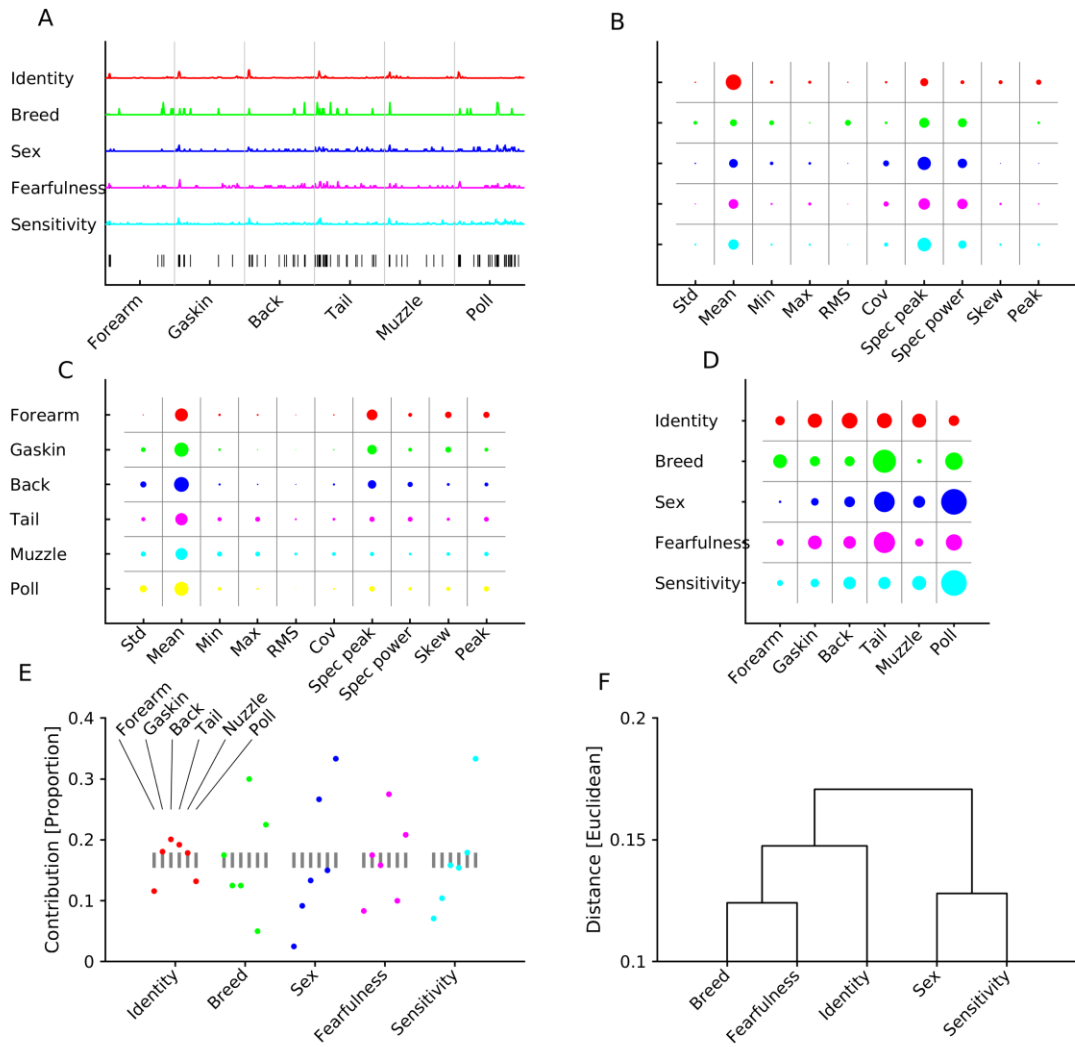
628 Figure 2



629

630

631 Figure 3



632

633

