



# Social information in equine movement gestalts

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## Abstract

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

**Keywords** Animal communication · Movement gestalt · Signal evolution · Phylogenetic ritualization · Horse cognition

## Introduction

Horses are well known for their highly developed perceptual abilities of processing movement patterns (Budiansky 1997; Murphy and Arkins 2007), an ability that may allow them to make inferences about the intentions and motivational states of conspecifics and, after domestication, their human caretakers (Pfungst 1907). We were interested in the origins of these advanced perceptual abilities in domestic horses. We reasoned that their evolution must have emerged from richly available postural information and movement gestalts, naturally produced by conspecifics during daily activities in

this highly social species (Laidre and Johnstone 2013). To our knowledge, close to nothing is known about the kind of information naturally available from horses' body movements, despite the likely importance of this channel of information for the evolution of perceptive abilities.

In our study, we investigated whether and how intrinsic and context-unspecific movement patterns in freely moving domestic horses convey social information. Over evolutionary times, horses have presumably been exposed to high predation pressure, with no real antipredator strategies apart from rapid flight (McGreevy 2004). The ability to recognise and interpret others' movement patterns may be particularly beneficial in such species due to the low signal-to-noise ratio and large variance in information content, a coding strategy that follows subtlety rather than conspicuousness (Laidre and Johnstone 2013). It is also likely that, for similar reasons, the evolution of a rich signal repertoire to coordinate social interactions was equally prevented to avoid attracting predators (Budiansky 1997), especially if alternative modes of information transfer were already effective. One hypothesis, therefore, is that natural selection has favoured alternative ways of enabling social coordination, bypassing the evolution of dedicated acoustic or visual signals especially at close range, as commonly found in non-human primates (Arbib et al. 2008; Budiansky 1997; Laidre and Johnstone 2013). This is not to say that horses do not have a

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rich communication repertoire, but they may not rely much on this ability when travelling or when exposure to predation is elevated for other reasons.

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

Accelerometers have already been used in studies of animal behaviour (Gerencser et al. 2013; Graf et al. 2015). To our knowledge, however, the previous studies have been based on data from one sensor only, which are unlikely to capture the complex nature of animals’ movement patterns. By positioning six inertial sensors at different body locations, we sought to collect data to determine more complex gestalt profiles, a holistic processing method common in studies of face perception (Dahl et al. 2007; Tanaka and Farah 1991), forensic analysis (Vogelsang et al. 2017) and Chinese character recognition (Mo et al. 2015). Accelerometers have also been used in horses to address a range of applied problems relating to health, anomalies and performance, such as to detect lameness (Keegan et al. 2002; McCracken et al. 2012; Starke et al. 2012; Thomsen et al. 2010), analyse rhythmical movements of horse and rider, jumping patterns or gait (Burla et al. 2014; Barrey and Galoux 1997), compare hoof ground impact on different surfaces (Ryan et al. 2006; Thomason and Peterson 2008) and horse shoes (Dyhre-Poulsen et al. 1994) and evaluate racing abilities (Leleu et al. 2005).

Here, we were interested in a more basic scientific problem, that is, whether horses could extract social information from observing others’ movement patterns. We focussed on a few very basic social parameters, i.e., identity, breed, sex, fearfulness and sensitivity. Horses can individuate conspecifics from their signal production across domains (audio–visual) (Proops and McComb 2012; Proops et al. 2009) and are sensitive to others’ facial expressions (Wathan and McComb 2014; Wathan et al. 2016), but it is not known whether these abilities generalize to movement patterns. While we think

it is likely that this is the case, the main purpose of our research is more to demonstrate a principle, which is that naturally available social attributes could be identified through movement patterns.

## Materials and methods

### Subjects

Subjects were 26 healthy horses of warm-blooded and cold-blooded breeds. We used 15 warm-blood breed individuals (2 stallions, age range (years):  $M = 13.5$ ,  $\min = 13$ ,  $\max = 14$ ; 6 geldings, age:  $M = 6.5$ ,  $\min = 5$ ,  $\max = 9$ ; 7 mares, age:  $M = 7.43$ ,  $\min = 5$ ,  $\max = 17$ ) and 11 cold-blood breed individuals (4 stallions, age:  $M = 7.5$ ,  $\min = 5$ ,  $\max = 11$ ; 2 geldings, age:  $M = 8$ ,  $\min = 6$ ,  $\max = 10$ ; 5 mares, age:  $M = 6.4$ ,  $\min = 2$ ,  $\max = 10$ ). None of the individuals suffered from any orthopaedic or neurological disorders.

### Data collection

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

### Preparation phase

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

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

### Habituation phase

The horse was free to explore the arena and habituate to the new environment for about 5–10 min. It also served the purpose to establish initial contact between the horse and the experimenter.

### Sensor synchronization phase

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

### Sensor attachment phase and experiment initiation

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

### Data analysis

We collected inertial data via custom-made miniature loggers, allowing to record tri-axial accelerometer, gyroscope and magnetometer data. For the analysis we focused solely on the accelerometer output [ $\pm 8$  g, 16 bit,  $\pm 4800$  LSB/g (accel sensitivity)]. Sensors were factory-calibrated. Inertial sensors were controlled by Arduino Pro Mini 328, 5V/16 MHz micro-computers. Data loggers were temporally aligned by manually moving them rapidly in directions of

all three axes and simultaneously filming them. In addition, we read out time stamps via a real time clock. We read out data at 128 Hz onto a SD card and later downloaded data files onto a PC for analysis.

### Data pre-processing and feature extraction

We first applied feature scaling to the raw values of each sensor and each axis by bringing all values into a range of [0, 1]. We then aligned these values and merged them to one file per individual, representing the unity-based normalized acceleration values of all sensors and all axes as a function of time. For each individual we extracted 100 non-overlapping segments at random points in time. Each segment consisted of 128 samples, equivalent to 1 s. For each of these segments and on all axes ( $a_x$ ,  $a_y$ ,  $a_z$ ,  $a_x/a_z$ ,  $|a|$ ) we extracted statistical features as follows: (1) standard deviation; (2) mean; (3) min; (4) max; (5) root mean square (rms); (6) auto-correlation: height of main, height and position of second peak; (7) spectral peak features: height and position of first six peaks; (8) spectral power features: power of five adjacent frequency bands (edges: 0.5, 1.5, 5, 10, and 20 kHz); (9) skewness; and (10) peaks: number, std (width), and std (prominence). Importantly, the  $a_x/a_z$  component reflected the tangent of the cranio-caudal direction relative to the ground. The acceleration magnitude ( $|a|$ ) was equal to the  $\sqrt{x^2 + y^2 + z^2}$ . In total, we calculated 105 features for each sensor, hence 630 features for each 1-s segment. All features were normalized to a range of [0–1] (Supplementary Figure 1E). A similar approach on feature extraction has been used in quantifying movement of freely ranging dogs (Gerencser et al. 2013).

### Classification algorithm

We used SVM, a supervised learning algorithm, to classify these segments. An SVM classification routine encompasses a training phase, during which a model will be derived that best separates samples of two classes, and a testing phase, during which the model will be evaluated by determining the performance on novel samples. We used the libsvm toolbox (Chang and Lin 2011) for implementing the SVM algorithm. Inputs to the SVM algorithm were pre-determined 630-element feature vectors, as described above, split into 80% (160) training and 20% (40) testing samples. In the SVM algorithm we used a radial basis function (RBF) Kernel. The two unknown parameters, the soft margin ( $C$ ) and the kernel parameter (gamma) (Cortes and Vapnik 1995), were determined in a fivefold cross-validation procedure on dedicated smaller numbers of samples, trading classification errors penalty for stability and thus leading to a higher degree of generalization rather than over-optimization.  $C$  and gamma were determined individually for each comparison. We then fed all training

samples as well as their labels, the correct classification outputs, into the SVM algorithm to generate the best fitting model. All testing samples, i.e., unknown, novel inputs, were then fed into the model, predictions obtained by the model and compared to the desired output.

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

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

### Feature selection

It is important to note that classification performance is generally influenced by the number of feature dimensions. Therefore, in a second step, we aimed at optimising the model by reducing the feature dimensions to avoid overfitting to irrelevant dimensions (noise), save storage space and reduce computation time. We, therefore, implemented two methods: (1) feature selection using a filter approach: with this approach we relied on the statistical features of our data by calculating  $t$  tests for each feature between the samples of the two classes of interest (Jafari and Azuaje 2006; Liu et al. 2004). This procedure resulted in  $p$  value for each feature dimension reflecting the effectiveness of features for those two classes. (2) Sequential feature selection: on top of a selected subset of features individual feature dimensions was added (forward search) until there was no further improvement or a maximum of 20 features was reached (Li et al. 2004; Resson et al. 2005). We use a hybrid method by combining these two approaches by first selecting statistically important feature dimensions and then sequentially searching for the best combinations of features (Fig. 2a). In this training period, we also applied a fivefold cross-validation routine. Figure 2a shows the means of all features (grey dots) and the 20 most discriminative features (blue circles) of two horses (ID1 vs. ID2). As can be seen, the features selected deviated strongly from the diagonal line, indicating different expressions of those particular features for the given classes.

### Control condition

We also calculated a performance baseline, which was determined by random labelling of training samples while maintaining the remaining processing routine as described above. Reported in Fig. 1 are the performance scores after the hybrid method for feature selection. We further calculated the probability of statistical feature types among the selected features as a function of attribute (‘identity’, ‘breed’, ‘sex’, ‘sensitivity’, ‘fearfulness’) and anatomical sensor position (‘forearm’, ‘gaskin’, ‘back’, ‘tail’, ‘muzzle’, ‘poll’). To calculate whether correct classification occurred more often than incorrect classification, we used  $\chi^2$ -tests of independence. We, therefore, compared the correct classification (observed values, see diagonals in Fig. 1a, c, e, g, i) with an expected outcome of 50%. We calculated proportional contribution of features for each attribute and each anatomical location (Fig. 3a–e) and used a hierarchical clustering algorithm to illustrate the similarity of gestalt profiles (Fig. 3f).

### Statistical tests

We used Chi-square tests of independence to evaluate whether there was a significant association between the correct and incorrect classifications for all attributes.

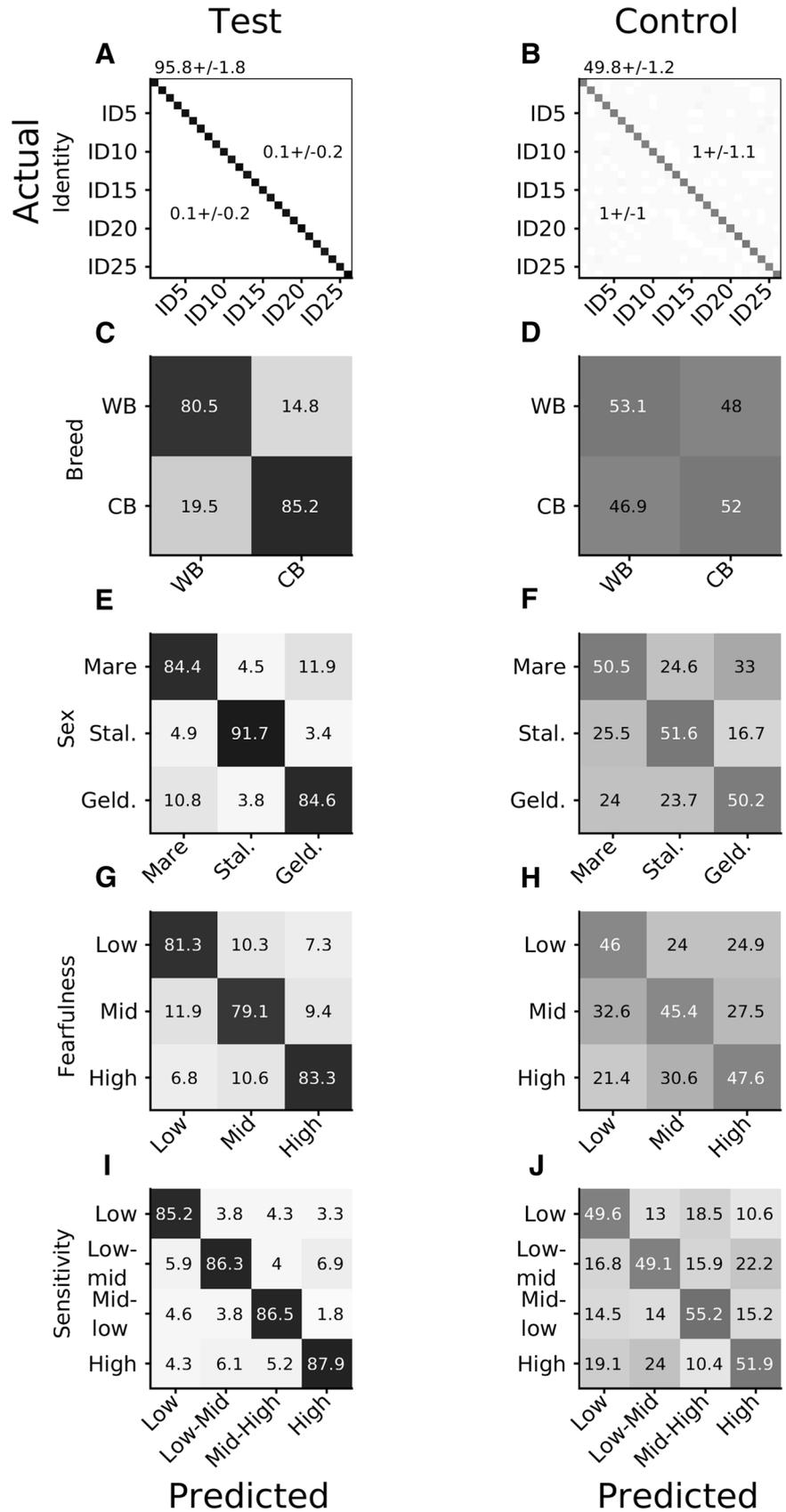
### Personality traits

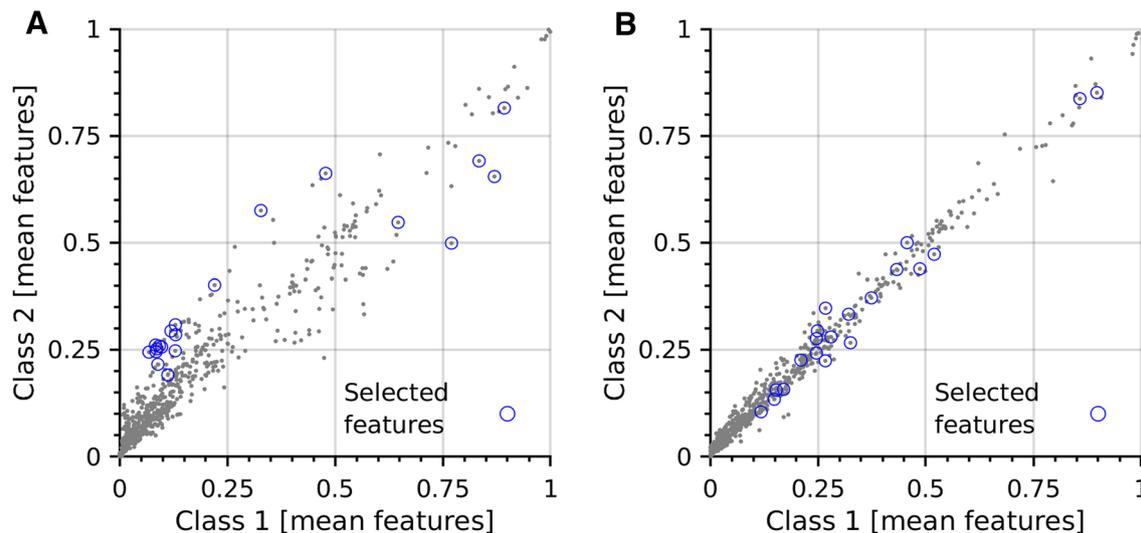
Aside from the intrinsic information (‘identity’, ‘breed’, ‘sex’) we included two personality traits (‘sensitivity’, ‘fearfulness’) in our analysis. These traits were measured in separate experimental sessions and are parts of the complete personality tests (CPT) (Lansade et al. 2016).

### Tactile sensitivity

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

**Fig. 1** Confusion matrices of classification outcome. Matrices **a, c, e, g, and i** show the actual test conditions for the attributes ‘identity’, ‘breed’, ‘sex’, ‘fearfulness’ and ‘sensitivity’. Matrices **b, d, f, h and j** show the control conditions. Each confusion matrix shows the ‘actual’ outcome (y-axis) against the ‘predicted’ outcome (x-axis). Percentage correct classifications are indicated on the diagonal line in each confusion matrix. Colour codes indicate the percentage correct classification with 100% in black and 0% in white





**Fig. 2** Feature evaluation. **a** Feature selection for classification of ID1 vs. ID2. Grey dots illustrate the mean values of features for ID1 (x-axis) vs. ID2 (y-axis). The blue circles mark the features selected

by our hybrid feature selection procedure. **b** Feature selection for classification of 'Mare' vs. 'Stallion'

## Fearfulness

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

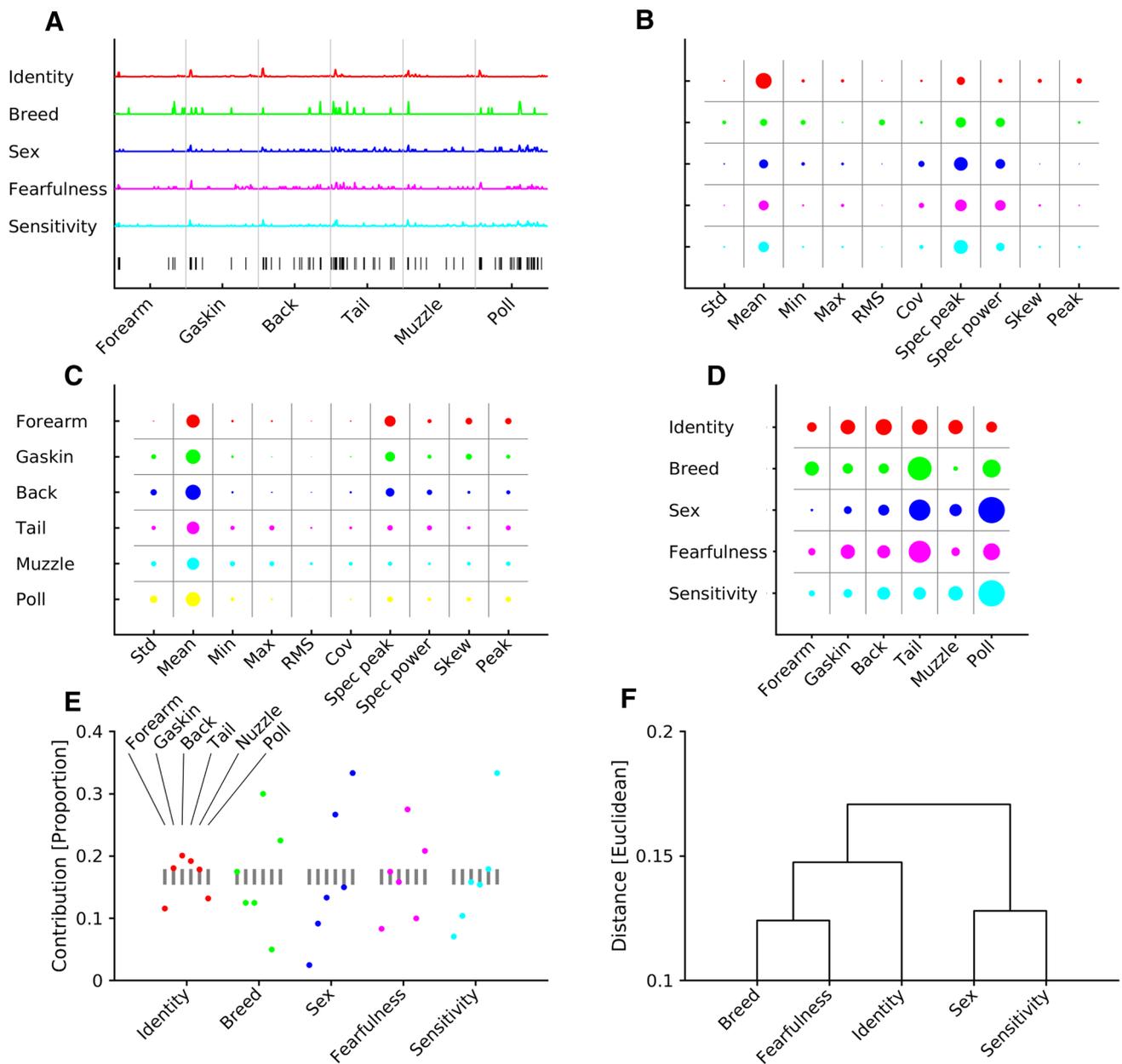
## Results

Our model was able to classify 'identity' at 95.8% (Fig. 1a), 'breed' at 82.9% (Fig. 1c) and 'sex' at 86.9% (Fig. 1e) correct classifications. The two personality traits 'fearfulness' and 'sensitivity' were classified correctly at 81.2% (Fig. 1g) and 86.5% (Fig. 1i), respectively. We contrasted these classification results with a randomly expected outcome (control condition). The randomly expected outcome was 50% correct classification due to SVM's pairwise comparisons. The actual performance of the control model was as follows: 'identity': 49.8% (Fig. 1b); 'breed': 52.6% (Fig. 1d); 'sex': 50.8% (Fig. 1f); 'fearfulness': 46.3% (Fig. 1h); 'sensitivity': 51.4% (Fig. 1j). We found that, in all test runs, occurrences of correct classifications (i.e., when the predicted outcome matched the actual outcome) were significantly higher than incorrect classifications (i.e., when the predicted outcome did not match the actual outcome) (Table 1). This was not the case in the control conditions, as expected, ruling out

idiosyncratic response patterns in the test runs not due to the attributes under investigation. The largest portion of misclassification was in the attribute 'sex', where geldings and mares were mutually misclassified more often than expected. We found a difference in geldings being more often misclassified as mares (11.9%), and vice versa (10.8%), compared to the expected level of misclassification (7.85, 7.65%): ( $\chi^2(1, N=100) = 13, p = 0.001$ ).

## How is information conveyed?

To determine which of the extracted features accounted for the high classification rates, we analysed the outcome of the feature selection procedure prior to classification (see "Materials and methods" and Fig. 2a, b). We were interested in the explanatory power of the statistical features with regard to attributes and anatomical locations (Fig. 3d). Overall, the means of the signal elements in any of the three axes as well as the spectral peaks and spectral power played the most crucial roles (Fig. 3b, c), as visualized by the size of the circles. The importance of these features, however, slightly varied depending on the attribute (Fig. 3a, b). While 'identity' could be explained to a large degree by variances in the means of the signal elements, 'sex', 'fearfulness' and 'sensitivity' could be best explained by a combination of spectral features and statistical means (Fig. 3a, b). The attribute 'breed' was best described via contributions of the means, spectral features and the statistical mean of the squares of the signal elements (RMS). Importantly, for each attribute a combination of distinct locations (sensors) contributed to correct predictions (Fig. 3a, d). While 'identity'



**Fig. 3** Explanatory power of features and locations. **a** Feature probabilities for each anatomical location (x-axis) and attribute (y-axis). Grey vertical lines separate the six locations (sensors). Each separation contains 105 features (see “Materials and methods”). Probabilities are only implied. Black vertical lines indicate the cumulative probabilities across attributes. **b** Probability of feature types (x-axis) by attributes (y-axis). Large circles indicate high probabilities, smaller circles low probability. **c** Probability of feature types (x-axis)

by anatomical locations (y-axis). **d** Average feature probability per anatomical locations (x-axis) and attributes (y-axis). **e** Contribution (feature probability) for each attribute (as in **d**) compared with random distribution (grey bars). Each bar shows the range of two standard deviations (95.4% of the variance). **f** Similarity of gestalt profiles. The heights of the inversely u-shaped elements in the tree indicate the Euclidean distance between the two profiles being connected

could be best accounted for by a combination of sensors at all anatomical locations, ‘breed’ and ‘sex’ were predominantly described by the poll and the tail in combination with other locations of minor importance. The personality trait ‘fearfulness’ was best detectable via the gaskin, the poll and the tail, depicting a different configuration of anatomical

locations than ‘sensitivity’, which mainly differentiated via the sensors at the head (poll and muzzle), the back and the tail. The importance of the sensory configuration is further highlighted in Fig. 4a.

We further compared the resulting gestalt profiles by calculating a hierarchical cluster tree (Fig. 3f). It turned out that

**Table 1** Statistical values for all attributes evaluated using Chi-square tests of independence

	$\chi$ -test	<i>p</i> -val test	$\chi$ -control	<i>p</i> -val control	<i>df</i>
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

‘breed’ and ‘fearfulness’ built one pair of close similarity and ‘sex’ and ‘sensitivity’ built another. ‘Identity’, however, due to a more equal contribution of all anatomical location, fell into its own class. In the next step we determined the degree to which each of the anatomical location differed from a random allocation of features to the six locations (Fig. 3e). In other words, do contributions of individual anatomical locations to the classification outcome deviate from a random distribution of features, where all locations contribute equally? We found that all (but two) locations were significantly different from the random distribution at a significance level of 5% (Fig. 3e: two standard deviations of random distribution shown in grey). Importantly, each attribute showed a set of locations that was over-represented (above the grey vertical bars in Fig. 3e), hence contributing positively to the classification outcome, and another set that was under-represented (below the grey vertical bars in Fig. 3e), hence being an unreliable source of information for that attribute. Figure 4b shows the under- (green circles) and over-represented locations (red circles) visually.

## Discussion

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

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

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

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

## Is movement perceived as information?

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

The following theoretical arguments, however, suggest that horses are expected to access information generated by movement patterns. First, movement patterns are readily available in this species, regardless of context. Information can thus be produced at virtually no extra costs, much in contrast to ritualised signals, and this may also provide less of a demand on receiver cognition. Second, feral horses are adapted to open grassland habitats, where the visual domain plays an important role, in contrast to visually dense forest habitats. Indeed, the acoustic repertoire of horses is relatively small, consisting of mainly four types of vocalizations (whinny, nicker, squeal, and roar) (Kiley 1972). Visual cues, such as facial expressions (Wathan and McComb 2014; Wathan et al. 2016), are visible only in close proximity, suggesting that movement patterns may be more efficient for information transfer at large distances. In contrast to other ungulates, social dominance in horses is not determined by size or weight (Duncan 1992; Feh 1990), but by social factors, such as age and migration status (Monard and Duncan 1996). Overall, we find it plausible that movement patterns play a role in horse communication, a hypothesis that has already been put forward by early work on animal cognition (Pfungst 1907).

In our study, we assumed that, similarly to face discrimination (Dahl et al. 2016; Fific and Townsend 2010),

the neural machinery of kinematic gestalt processing in mammals processes limb movements in a non-linear space by which the relevant features are extracted from a high-dimensional space and then processed in a parallel coactive fashion. This processing is a reasonable assumption to support the demand for efficient neural processing that can potentially allow for rapid decision making. One way to optimise the representational embedding of kinematic features is by reducing high dimensionality to a subspace that represents most kinematic variance. Reducing dimensionality, therefore, reduces processing time and storage space. To simulate this biologically plausible process, we optimised the feature selection process using a sequential feature selection approach, selecting the 20 features that sequentially add most of increment in correct prediction.

### Social information from movement

Our choice of social attributes (identity, sex, breed and personality factors) was practically and not theoretically motivated, mainly due to ease of accessibility. Our goal was to demonstrate the principles of a new methodology, but we predict that social information contained in movement patterns goes beyond the small number of attributes we chose in this study. Nevertheless, the current attributes may have relevance in wild horses in the following ways. First, attributes such as identity, sex or breed (representative of morphological features) may be important in rapid assessments by stallions in their attempts to monopolise a group of mares. While mares tend to lead social groups to resources, stallions tend to follow in the rear (Briard et al. 2017), suggesting that rapid identification at larger distances is essential for them. Similar arguments could be made for mares, if there is a danger of infanticide by out-group males. Furthermore, personality traits, such as fearfulness, may be important in rapid assessments of unfamiliar rivals or sexual partners (Linklater et al. 2000; McDonnell and Haviland 1995; Miller and Denniston 1979).

### A quantitative approach to ethology

Ethology aims to address biological questions about animal behaviour in natural conditions. The classic methodological approach has always been to first determine a species' behavioural repertoire, the 'ethogram', to code behavioural elements according to different sampling regimes (Altmann 1974). Although this has been an extremely successful and productive approach, its main weakness is that behavioural elements are subjectively coded by human observers, rather than by objective

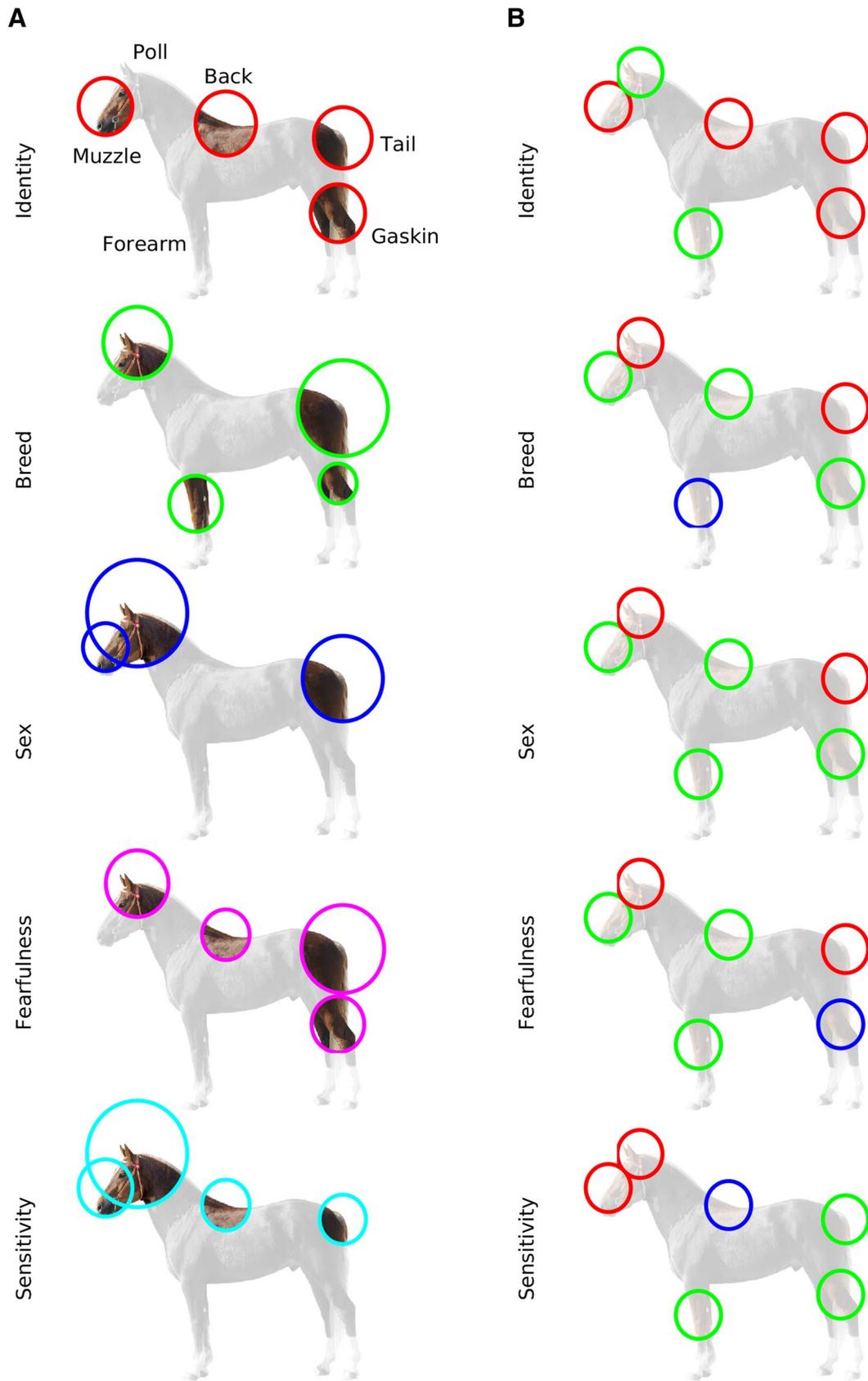
measurements. The difficulties of this approach is well illustrated, for example, in ape gestural studies, where observational studies on gesture repertoires of wild chimpanzees can generate wildly different results [ $N = 66$  gestures (Hobaiter and Byrne 2011, 2014);  $N = 30$  gestures (Roberts et al. 2012)], even if collected from the same community. Thus, the quest to standardize behavioural repertoires is a challenging task and recording the full behavioural repertoire of a species via traditional ethograms is nearly impossible, and even partial descriptions of repertoires are extremely time-consuming and highly subjective.

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

### Conclusion

In this study we showed that movement patterns of freely moving animals contain a large amount of socially relevant information, which potentially can be accessed by conspecifics. Information transfer via movement patterns, therefore, follows a principle of subtlety rather than conspicuousness, a principle of information transfer in animals which is largely unexplored.

Furthermore, our study offers a new tool to investigate behavioural patterns in a wide range of animals. Bio-logging via inertial sensor techniques replace video camera recording and its extensive analysis procedure. An expert system, as presented here, helps automating ethological investigations in that it classifies movement patterns of freely moving animals into meaningful classes. Future directions might incorporate unsupervised learning algorithms, implying that no a-priori assumption about attribute labels is required.



**Fig. 4** Gestalt profiles. **a** Relative contribution of sensors at given anatomical locations is represented in the sizes of the circles, with increasing size indicating greater relative importance. Shown are the locations that together explain more or equal than 70% of the cumulative contribution of locations, starting with the location with the largest contribution. **b** Each attribute is described by the locations (circles) that contributed more (red) or less (green) than expected by an equal contribution of all locations. Blue circles show the locations that fell into the expected range of equal contribution

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## Compliance with ethical standards

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

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

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