

The importance of syntax in a dynamic visual signal: recognition of jacky dragon displays depends upon sequence

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Abstract It is well established that recognition of complex acoustic signals, such as bird song, is dependent upon the temporal ordering of signal units or syntax. Much less is known about functionally analogous visual displays. The jacky dragon (*Amphibolurus muricatus*) is a native Australian agamid lizard with a highly stereotyped visual display made up of three discrete motor patterns. We conducted a playback experiment using high-resolution computer animations of conspecifics to test the importance of temporal order for signal efficacy. Lizards were shown three different life-sized simulated animations of conspecific differing in their skin texture and morphology signatures ranging from highly natural to abnormal. We evaluated signal recognition and assessed the relative importance of syntax and morphology. Our results showed that signal recognition is highly sensitive to syntax and this largely determines the observers' behavioural responses. Stimuli with abnormal texture and shape were highly effective, as long as the natural order of motor patterns was preserved. Display recognition in jacky lizards hence depends upon syntax in just the same way as temporally constrained signals in other modalities.

Keywords Jacky dragon · *Amphibolurus muricatus* · Syntax · Morphology · Visual display · Computer animation

Introduction

The design of signals used by animals to communicate reflects selection for characteristics that maximise signal's transmission and efficiency to stimulate the sensory system of intended receivers (Endler 1992; Clark and Uetz 1993; Endler 1993; Bradbury and Vehrencamp 1998; Rowe 1999; Ryan and Kime 2003; Ord and Stamps 2008). If a signal is composed of multiple components, then the sequential organisation of these elements is often critical for successful communication. Marler and Peters (1988) defined the temporal ordering of the signal units as segmental syntax. In human language, syntax is a function of grammatical structure, which aids in the understanding of verbal communication (Wierzbicka 1996). However, modifications in words order may still successfully convey the general context of ideas and overall meaning (Wierzbicka 1996). Unlike semantic connotations associated with the understanding of human language (Nowak et al. 2000), the distinction between semantics and syntax is that syntactical order of animal signals is temporally constrained by particular selective features on design (Hailman et al. 1987; Holland et al. 2000).

The parallels between human language and nonhuman communication in the importance of syntax, named phonological syntax (Marler 1977), are numerous; consequently, the role of temporal organisation of signal components has mostly been considered in avian communication (Marler 1977; Hailman 1986). In particular, a significant endeavour has been directed towards examining syntactical structure in different avian communication contexts like song learning (Balaban 1988a; Okanoya and Yamaguchi 1997; Podos et al. 1999), development and evolution of songs (Okanoya et al. 2000; Soha and Marler 2001), geographical variations (Balaban 1988b; Pytte 1997; Päckert et al. 2003; Sung et al. 2005), territoriality (Nowicki et al. 2001), mate choice (Ballentine et al. 2003), and conspecific or group recognition (Brindley

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1991; Briefer et al. 2013). However, despite the growing knowledge on the importance of syntax in acoustic communication, the analogous phenomenon of temporal arrangement of signal units in dynamic visual signals is still poorly understood.

Broadly, the general syntactical rules of communication are expected to be implicit when the temporal arrangement and composition of signal units in a particular sequence produce a contextual meaning (Marler and Peters 1988), such as providing relevant information about an individual's status (Hailman et al. 1985, 1987) or about the level or nature of predation risk (Templeton et al. 2005). Commonly, normal segmental syntax follows a predictable Markovian chain sequence (Rusch et al. 1996; Leonardo and Konishi 1999), in which each signal unit depends on the unit that directly precedes it. However, the temporal reorganisation of signal units may change the way that signals are perceived in one of two ways. If the temporal structure of the signal sequence is altered, the results may be either a different “message” (Smith 1977; Podos et al. 1999; Arnold and Zuberbühler 2006) or a complete failure of recognition (Marler 1977; Kreuzer and Bremond 1989).

The design characteristics of the visual displays in the repertoire of the jacky dragon (*Amphibolurus muricatus*), an endemic species to southeast Australia (Harlow and Taylor 2000; Warner and Shine 2008), and the displays' role in mediating social interactions have been the focus of several studies (Ord and Evans 2002; Peters and Evans 2003; Woo et al. 2009; Woo and Rieucou 2012; Woo and Rieucou 2013). Jacky dragons produce highly stereotyped visual displays (Carpenter and Ferguson 1977) that are composed of three discrete motor patterns, arranged in a semi-Markovian series (Peters and Ord 2003). The complex visual displays that constitute the signalling repertoire of *agamid* and *anolis* lizards, termed display action patterns (DAPs), are characterised by distinct changes in body position over a period of time (Carpenter and Ferguson 1977; Jenssen 1977; Martins and Lamont 1998). Typical jacky dragon's DAPs begin with an initial alerting component consisting of a tail-flick (Peters and Evans 2003), followed by a backward-forward arm wave and concluding with a push-up body rock (Peters and Ord 2003) (see Fig. 1). Push-up body rocks are often performed during various social interactions such as male-male contests, territoriality or courtship (Carpenter et al. 1970). By controlling the displayed behaviour produced by a simulated opponent (submissive or aggressive displays) in a way that matched or deviated from the strategic responses of subjects (submissive or aggressive), Van Dyk and Evans (2008) showed that the outcomes of male-male interactions are highly sensitive to the nature of the displays presented sequentially. However, it remains to be solved whether the visual signal syntax per se (i.e. the particular temporal arrangement of the signal units—discrete motor patterns) is an important feature in jacky dragon's signal design and efficiency. In an early study,

Jenssen (1970) showed that video footages of reversed DAPs lacked to elicit responses from females *Anolis nebulosus*. However, to date, direct manipulation that is aimed at examining the role of syntax in the dynamic motion-based signalling of jacky dragons is lacking.

By conducting a video playback experiment using computer-generated animations of life-sized demonstrators, we tested the hypothesis that syntax and morphology are critical features for signal efficacy and recognition in the jacky dragon. We created three different morphological models and presented each with either “natural” syntax or “unnatural” reversed syntactical structure. If recognition is dependent on syntactical structure, then natural syntax should be most effective for eliciting social displays. By pitting morphology and syntax against one another, we assessed the relative importance of these cues during motion-based signalling in jacky lizards.

Materials and methods

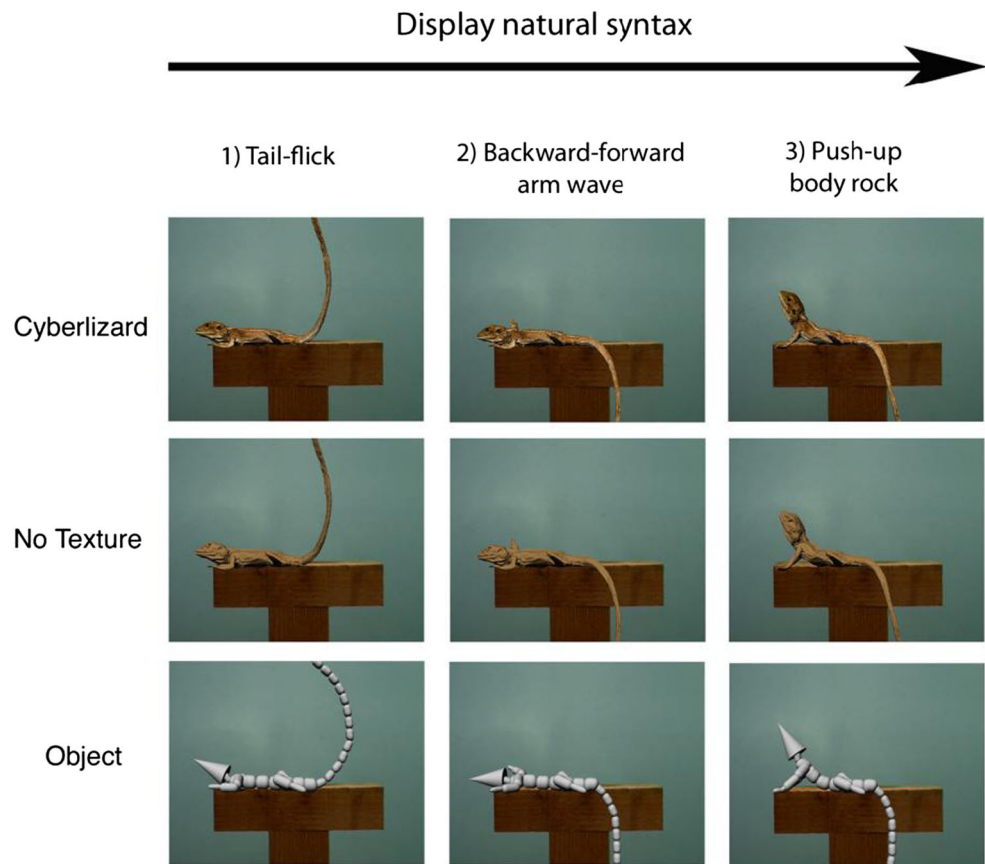
Subjects

Twenty male jacky dragons were collected from Lane Cove, La Perouse and Royal National Parks in regional Sydney, NSW, Australia and were maintained in individual enclosures (64×75×120 cm) in captive facilities at Macquarie University. Each enclosure was constructed with three opaque walls, and one panel of Perspex to enable playback presentations and video recording. Each enclosure included tree branches and stumps for perch, leaf foliage and a sandy substrate. The subjects were fed with live crickets (*Achetus domesticus*) twice a week that we dusted with vitamin supplements (RepCal) and given water ad libitum. We maintained lizards under a 14:10 h L/D cycle with additional heat lamps (125 W Spotone, Philips) for 10 h/day, with ultraviolet (UV) lamps (300 W Ultra-Vitalux, Osram) that were illuminated for half an hour in the morning.

Stimulus acquisition

As the temporal basis for our animation sequences, we obtained population estimates for the mean duration of motor patterns in previous studies (Woo et al. 2009; Woo and Rieucou 2012). As display duration was found to be critically important in jacky dragons (Peters and Evans 2003; Woo and Rieucou 2012), we measured the duration as the total number of frames for each display from the onset of the signal to its completion. We randomly selected tail-flicks (TFs) and push-up body rocks (PUBRs) for measuring the duration of population-typical displays from archival video footage (Ord and Evans 2002; Van Dyk and Evans 2007). From these samples, we selected population-typical durations for TF

Fig. 1 Representative frames for each stimulus model and corresponding motor pattern within the display. The *black arrow* indicates the natural syntactical order of the visual signal



(mean \pm SD=49.67 \pm 45.44 frames) and PUBR (mean \pm SD=12.57 \pm 3.37 frames) clips to use for stimuli. Peters and Ord (2003) found that the push-up always precedes the body rock, and that the backward-forward arm wave (BFAW) always precedes the forward movement. We therefore combined the push-up body rock and the backward-forward arm wave as units for manipulation of syntax. Moreover, as the BFAW almost always occurred at two frames, this duration was noted as population-typical within our video footage.

We identified and selected TF, BFAW and PUBR clips from the archival footage PUBRs (Ord and Evans 2002; Van Dyk and Evans 2007). From these videos, we sampled 30 outdoor and 74 indoor TF, BFAW and PUBR displays. These video samples served as model clips for our animation sequences in which we matched similarly the duration and movement patterns to those of real lizards.

Stimulus construction and computer animations

The construction details of the lizard stimulus were previously described in Woo (2007), Woo and Rieucau (2008) and Woo and Rieucau (2012). A taxidermic model was prepared after the natural death of one wild-caught jacky dragon. The model was then scanned using a Konica Minolta VI-9i camera (Konica Minolta Holdings, Inc., Japan) by New Dawn

(Bexley North, NSW, Australia) to create a 50,000 polygon model that we imported into Lightwave[®] 3D v8 (NewTek Inc., San Antonio, TX, USA).

Using Lightwave[®] Modeller, we added “skelegons” and skin texture to the object. “Skelegons” were created to mimic the spinal vertebrae (from the cervical to the sacral regions), the head and the limbs. We converted them to “bones” in Lightwave[®] Layout. We added the skin texture by photographing the skin of a real lizard, and applying the digital photograph to the outer layer of the object, which is termed “UV map.” This allows dividing the 3D object into 2D surface planes to allow exact areas on the model to be specified for the alteration of texture. We then carefully aligned the patterns photographed on the live body with the corresponding areas on the 3D animation model.

All of our constructed animation display sequences were rendered using Render Farm Commander v2.9.8 (Bruce Rayne, Lalor Park, NSW Australia), which allowed us to convert the scene created on Lightwave[®] 3D into individual Joint Photographic Expert Groups (JPG) frames. The render farm then distributed the production of large animation files across several computers that were connected across a network for increased efficiency. We imported the JPGs into Final Cut Pro HD (Apple Computer Inc.), which combined all individual JPGs into a single movie file (*.MOV), and

assembled each sequence for video playback experiments. We rendered all sequences for PAL-DV standard resolution (5:1 compression; horizontal resolution 575 lines; 25 frames s⁻¹).

We created three animated stimuli to test whether signal efficacy was sensitive to syntax (Fig. 1): (1) a lizard with normal morphology and typical skin textural features seen on a real individual (i.e. the Cyberlizard), (2) a lizard with normal morphology but without realistic skin texture (i.e. No Texture Cyberlizard) and (3) an object shaped like a lizard but lacking texture and presenting abnormal morphology (i.e. the Object). The animated lizard with normal morphology but lacking skin texture was created by removing the skin texture from the Cyberlizard. An average RGB value was calculated by selecting 30 random colour patches across the photographs taken originally to develop the skin texture. This was used to create a homogeneous surface. Lastly, the object without either morphology or skin texture was modelled after the basic jacky dragon computer-generated animation model, with the same bone structure. A capsule shape was constructed around each bone to allow for a one-to-one transition of object structure-to-bone, and the body segments were adjusted to match the approximate properties of a jacky dragon. The object hence retained a basic lizard shape, but lacked the typical morphology of the species. All three models were rotoscoped (Gatesy et al. 1999) to three different display action pattern exemplars to provide variation in the playback sequences and to avoid habituation to movement.

Experimental design

To provide the best opportunity for viewing complete displays, we designed the stimuli to be perceived by the lizards from a distance of one metre, and the animation stimuli appeared on a wooden perch, similar to Woo and Rieucau (2012) and Woo and Rieucau (2013). After each individual display, the animation returned to the original position, thus avoiding any awkward transitions in the played back sequence. Each sequence began with two minutes of an empty perch, followed by 10 min of a displaying stimulus. The entire duration of each sequence was 12 min. With the exception of control stimuli, each model produced a display every minute (i.e. ten displays in total). We created nine different stimuli in a 3×3 within-subject design (morphology×syntax). First, each of the three models was used to create a matching control stimulus (i.e. a still lizard or an object on perch). Each of the models was then used to match a display with normal syntax (i.e. the natural motor pattern: TF×BFAW×PUBR; see Table 1). Finally, the three models were each matched to a display with reverse syntax (i.e. the unnatural motor pattern: PUBR×BFAW×TF).

The video playbacks were presented using an iMac (Apple Computer Inc.), which subsequently projected the animation on a Sony Trinitron monitor (Model No.PVM-14N5A). A

Panasonic CCTV camera (WV-CP240/G) recorded all behavioural responses and was connected to a colour viewfinder monitor (Panasonic TC-1470Y), and consequently converted to MPEG4 format using EvolutionTV™ (Miglia Technology LTD).

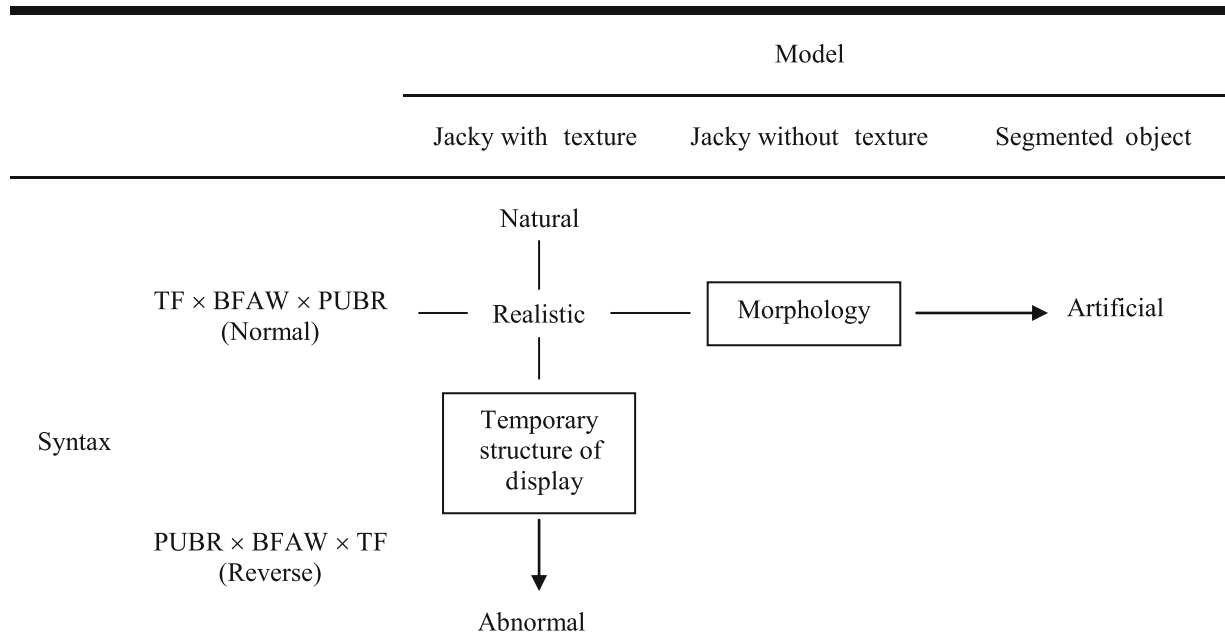
We tested each subject for an initial 9 days by randomising the order of the presented playback sequences. We then repeated testing for another consecutive 9 days, during which the stimulus sequence was reversed for each trial to counterbalance order effects. For each testing day, all lizards were exposed to only one of the treatments and each individual lizard was exposed to each treatment sequence (i.e. a morphology-syntax combination) twice across the whole experiment. Following the sequence order for counterbalancing, all the 20 lizards observed 18 sequences each, thereby a total of 360 trials were performed across the experiment. For each trial, we followed and counted the number of behavioural responses exhibited by the observer lizard.

Behavioural responses

During an initial pilot experiment on the same 20 lizards, we measured the probability of orienting responses towards either natural and unnatural (reversed syntax) motor patterns displayed by the Cyberlizard. Peters and Evans (2003) defined an orienting response as the observable redirection of the focal lizard's head towards the video sequence and orienting responses have been proven as reliable proxies during video playback experiments exploring visual signalling in jacky dragons (Woo and Rieucau 2012; Woo and Rieucau 2013). During the first part of the pilot experiment, each of the 20 lizards saw a unique randomly chosen 12-min long sequence (natural syntax, reversed syntax or control—a still lizard) per day (days 1, 2 and 3). The regime was after repeated for an additional 3 days (days 4, 5 and 6), during which the stimuli were shown to focal lizards but in reverse order to counterbalance for order effects. Therefore each lizard observed each treatment sequence twice, thereby a total of 120 stimuli were presented during the pilot experiment. For each sequence presentation, we scored whether or not an orienting response occurred. We found that all the lizards responded invariably, by orienting their gaze in the direction of the video monitor, to all sequences regardless their syntactical structure at the exception of the control sequences that did not elicit any orienting responses. Any statistical analysis became thus redundant. Our results suggest that sequences presenting either a natural or an unnatural syntax were equally conspicuous, and hence a more reliable measure was to account for behavioural responses.

Consequently, we followed the behavioural responses of the focal subject during each stimulus presentation. We recorded a total of six different behavioural responses that were directed towards the animation playback stimuli: tail-flick,

Table 1 Design of stimuli began with the most naturalistic model with of a jacky lizard with texture and changes in temporal display structure would create an abnormal sequence (i.e., reverse syntax)



Morphology was then transformed from a more realistic model to an animation that was artificial in shape but maintained temporal display characteristics

backward-forward arm wave, push-up body rock, gular expansion, slow arm wave and attack.

Data analysis

By conducting a principal component analysis (PCA) followed by Varimax rotation (Tabachnick and Fidell 2001) in SPSS 11 for Mac OS X (SPSS Inc., Chicago, Illinois USA), we identified which of the six displayed behaviours were correlated, and these displayed behaviours were subsequently grouped into different principal components (PCs). The PCA yielded three factors with eigenvalues greater than 1, accounting for approximately 75 % of the total variance (Table 2), and based on the scree plot, we grouped similar motor patterns into three distinct PCs. Displays with a loading greater than 0.32 were considered to contribute to a PC (Tabachnick and Fidell 2001). PC1 described aggressive displays and contained tail-flick, backward-forward arm wave, push-up body rock and gular expansion displays. PC2 contained the attack response while PC3 contained the submissive slow arm wave (see Table 2).

We used general linear models (GLMs) to examine the effects of syntax (two levels: natural and unnatural) and morphology (three levels: the Cyberlizard, the No Texture Cyberlizard and the Object), as well as an interaction between these two factors on the total number of behavioural responses exhibited by the focal lizards and on the correlated behaviours displays (PCs). Syntax and

morphology were treated as fixed effects in the GLMs and we included focal lizards’ identity as a random effect to control for pseudo-replication. Due to the absence of response induced by the control sequences (i.e. inanimate lizard), only the two syntax display treatments (natural and unnatural) were included in our analysis. GLMs were performed in SPSS 11.

Table 2 Results of the principal component analysis (PCA) grouping motor pattern displays into three principal components: PC1=aggressive (tail-flick, backward-forward arm wave, push-up body rock, gular expansion), PC2=attack and PC3=submissive (slow arm wave)

| Display | Principal components | | |
|------------------------------|----------------------|-------------|-------------|
| | PC1 | PC2 | PC3 |
| Tail-flick | <i>0.79</i> | 0.12 | 0.07 |
| Backward-forward arm wave | <i>0.97</i> | 0.09 | 0.01 |
| Push-up body rock | <i>0.95</i> | 0.09 | 0.01 |
| Gular expansion | <i>0.81</i> | 0.03 | 0.00 |
| Attack | 0.06 | <i>0.70</i> | 0.12 |
| Slow arm wave | 0.03 | 0.13 | <i>0.85</i> |
| Eigenvalue | 2.47 | 1.050 | 1.025 |
| Variance explained (%) | 41.17 | 17.50 | 17.09 |
| Total variance explained (%) | 75.76 | | |

Loadings, eigenvalues and explained variance are given for the three emerging principal components. Component loadings in italics indicate the main contributing displays to a component

Results

Syntax significantly affected the total frequency of behavioural responses produced by focal lizards ($F_{1, 215}=6.75, P=0.01$). We did not detect any significant effect of morphology ($F_{2, 215}=0.77, P=0.46$) on the frequency of behavioural responses. The interaction between syntax and morphology was not statistically significant ($F_{2, 215}=0.31, P=0.73$). Focal lizards produced more display responses to sequences with normal syntactical structure (natural motor pattern) compared with sequences with reversed syntax (unnatural motor pattern), regardless of the simulated demonstrator's morphology (Fig. 2).

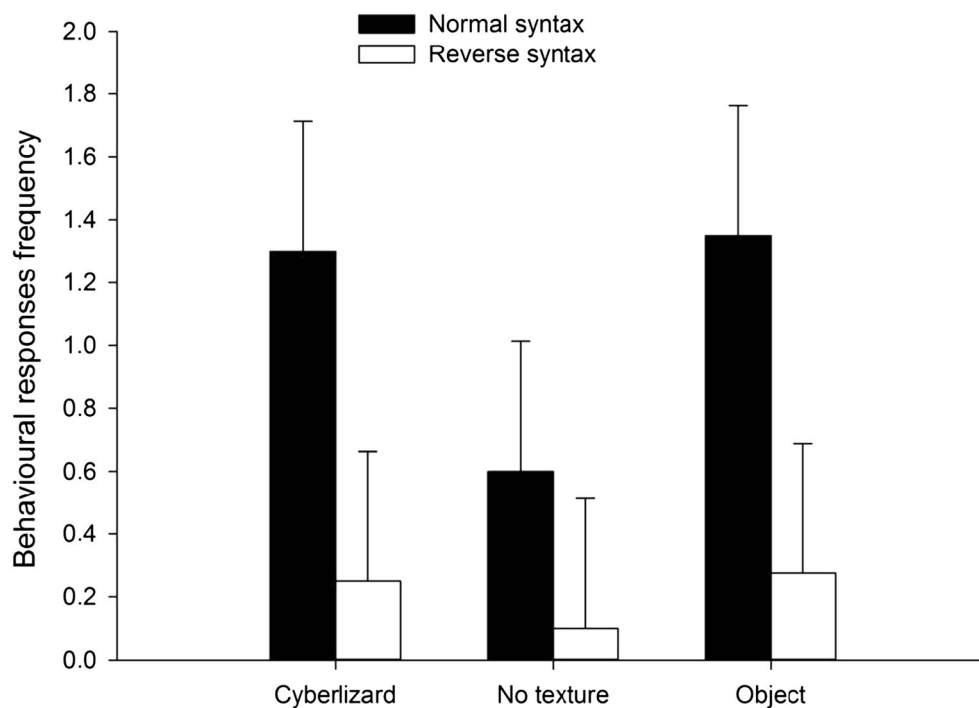
When separating the behavioural displays into the three correlated displays (PCs), we found a significant main effect of syntax on the frequency of submissive displays ($F_{1, 215}=4.71, P=0.02$), but no main effect of morphology ($F_{2, 215}=0.05, P=0.95$) and no significant interaction between these two factors ($F_{2, 215}=1.34, P=0.27$). Lizards produced more submissive displays when exposed to a motor pattern with a normal syntax (Fig. 3). Despite its failure to reach conventional level of statistical significance, there was a pattern towards more attack responses produced by lizards exposed to sequences with natural syntax compared with sequences with reversed syntax ($F_{1, 215}=3.55, P=0.06$). Morphology did not affect the frequency of attack displays ($F_{2, 215}=1.43, P=0.24$), and the interaction between syntax and morphology was not significant ($F_{2, 215}=1.29, P=0.28$). There was no significant effect of syntax ($F_{1, 215}=2.31, P=0.13$) or model's morphology ($F_{2, 215}=0.88, P=0.41$) and no significant

interaction between syntax and morphology ($F_{2, 215}=0.82, P=0.44$) on the frequency of aggressive display responses.

Discussion

Our study presented the first evidence of the role of visual syntax in a dynamic motion-based display. We demonstrated that the temporal arrangement of the visual signal units is a critical feature for signal recognition, irrespective of the morphological characteristics of the simulated conspecifics. Lizards responded with more social signals to sequences with natural syntax compared with sequences presenting unnatural syntactical structures (e.g. reversed DAPs). Similar to Jenssen's (1970) study, we found that by violating the temporal ordering of displays, lizards were not able to recognise a typical social display but were still sensitive to general movement as was observed in their orientation responses (pilot experiment). However, unlike Martins et al. (2005), who reported that southern sagebrush lizards (*Sceloporus graciosus*) match the irregular syntax of a DAP produced by a robotic lizard during playback experiments, we found that responses to stimuli were highly affected by syntax, with fewer responses produced when the syntax order was reversed. As jacky dragons have the ability to discriminate between familiar and unfamiliar video conspecifics based on morphological cues (Van Dyk and Evans 2007), we can exclude the possibility that this reflects discrepancies in the responses to the stimuli observed in our study. In contrast to the strong effect of syntax, morphological signature of the

Fig. 2 Frequencies of behavioural responses (mean \pm SE) exhibited by the focal lizards to normal and reversed syntax sequences across the three levels of morphology (Cyberlizard, no texture, object)



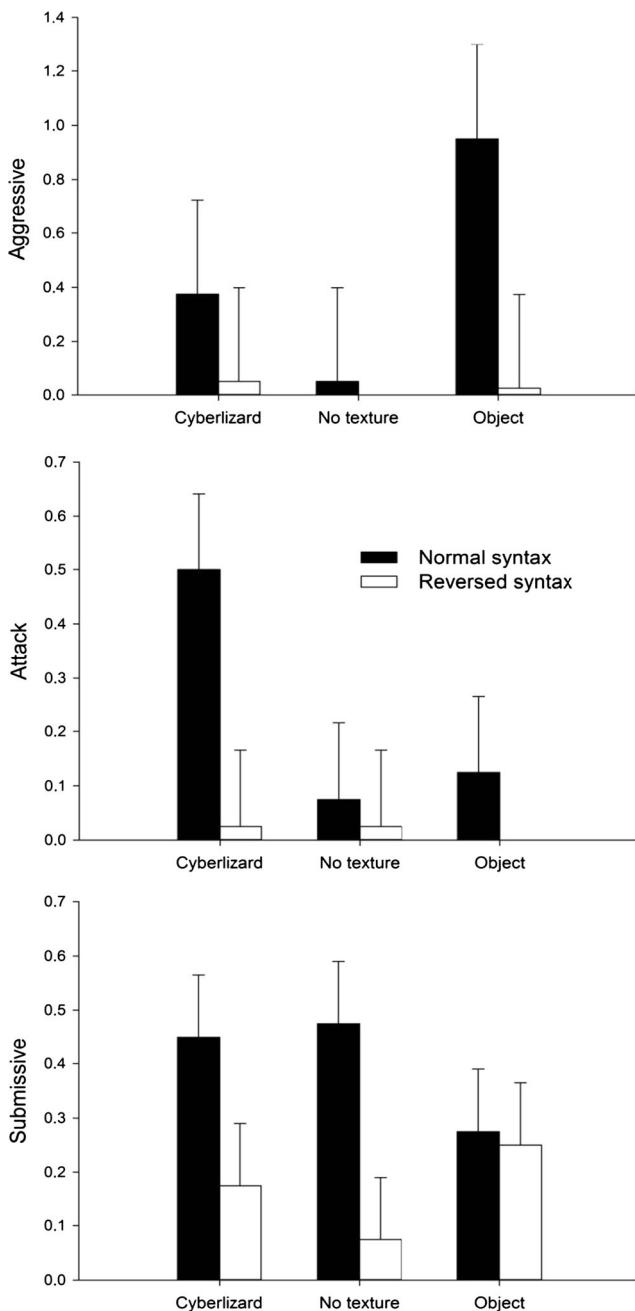


Fig. 3 Frequencies of aggressive, attack and submissive displays (mean \pm SE) to normal and reversed syntax sequences across the three levels of morphology

computer-generated animations did not affect the lizards' ability to recognise the motion signature of the displayed signals. Hence, our results suggest that signal recognition is likely dependent upon correct syntactical structure in the jacky dragon's movement-based signalling and is not based on morphology.

The results of our pilot experiment indicate that signal conspicuousness is not sensitive to signal syntax. Conspicuousness is critical for establishing initial contact with another

individual, such as the advertising function of the tail-flick (Peters and Evans 2003). However, if syntax modifications do not alter signal efficiency to draw the attention of intended receivers, changes in syntactical structure appear to modify the informative content of motion-based signals with important effects on the outcome of any social interactions. A visual signal with an unnatural syntax may be perceived as behaviourally irrelevant. Signal recognition is important for individuals that want to rapidly assess a conspecific's intentions or fighting abilities (Leal and Rodríguez-Robles 1997; Van Dyk and Evans 2008).

An intriguing result is certainly that the syntax of visual signals influenced focal lizards' social responses in different ways. The presentation of sequences with natural temporal order, regardless of the animations' morphology, induced more submissive and attack displays than unnatural syntax sequences. However, syntax did not affect focal lizards' propensity to aggressively respond to the animations. Yet, to date, we cannot clearly ascertain the functional basis of these response discrepancies. Interactive video playback experiments, similar to Van Dyk and Evans (2008), can provide an efficient means to further investigate the role of signals syntax on jacky dragons' strategic decisions to initiate/retaliate or retreat from agonistic situations. It is also conceivable that within our tested population, selected individuals may behave stereotypically and produce more aggressive, submissive, or attack responses. We note that a larger sample may also help us to fully elucidate the finer differences in behavioural responses that are elicited by dynamic syntactical sequences.

In our study, observer lizards were able to perceive models' morphological differences, even though such morphological differences did not influence the observers' behavioural responses. The discrimination of subtle cues as artefacts of the signal is common in acoustic communication. During field playback experiments, Carolina chickadees (*P. carolinensis*) produced response calls with different note composition when exposed to calls that follow normal syntactical orders compared with atypically ordered calls during Fall and Winter periods when chickadees generally form highly cohesive social flocks (Clucas et al. 2004). Moreover, when the syntax of calls was violated, birds responded to partial segments in typical call structures that were derived from complete abnormal atypical calls. Therefore, it follows from these results that note composition and order are important for successful social interactions, with atypical syntax losing their biological significance (Clucas et al. 2004). How jacky dragons perceive and act on changes in information content induced by subtle modification in signals' syntax remains to be further explored.

Competition from other species has been suggested as a constraint on the evolution of signal design. In acoustic communication, Nelson and Marler (1990) reported that songs from sympatric songbird species are divided in well-defined acoustic spaces. In *Anolis* lizards, species that cohabitate in

sympatric distribution ranges have similar communicative visual displays for territoriality and mating interactions, but have been found to exhibit variations in dewlap colour and morphology (Ord and Martins 2006; Nicholson et al. 2007). In contrast to the visual signals of *Anolis* lizards, species recognition and signal design in the jacky lizard has been free from the competitive pressures of sympatric species with similar signals. To our knowledge, no other competing agamids perform similar stereotyped displays suggesting that jacky dragons have developed a motion-based communicative repertoire specifically directed towards interacting with members of their own species. Other selection pressures may influence signal design and the necessity to maintain syntactical structure in this species, for example, visual noise from the environmental background scene (Peters et al. 2007; Woo and Rieucou 2013) or the potential trade-off between signal efficiency and production costs (Woo and Rieucou 2012).

This study provides new insights that contribute to the current knowledge on the design characteristics of signals used in lizard motion-based signalling. Our results also shed light on broad similarities between acoustic and visual communication regarding the role of signal syntax. However, more empirical works are necessary to ascertain the mechanisms that have shaped the particular temporal arrangement of jacky dragons stereotyped visual displays.

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