



Ancestral iconicity: the dance language of bees revisited

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ABSTRACT

The waggle dance of bees has given rise to some of the most striking and detailed studies of animal communication. But because of its gradient character, the waggle dance has widely been taken to have properties that are wholly distinct from those of human language. We argue that this is mistaken, and that the waggle dance represents the oldest instantiation of an iconic system also found in human language, notably in sign language. The waggle dance helps bees locate a food source through four properties: (1) food distance is conveyed through the duration of the wagging phase; and (2) food direction is conveyed through the orientation of the waggle run. In addition, (3) while in bees that dance horizontally, the waggle run points towards the food source, in bees that dance vertically the information involves transposition: the angle of the dance relative to ‘upwards’ is interpreted as the angle of the food direction relative to the sun. Finally, (4) the number of waggle runs increases with food quality. We show that properties 1 and 2 are instantiated in sign language classifier predicates, highly iconic constructions that produce visual animations of the orientation and movement of an entity. Furthermore, classifier movement (property 3) can be interpreted either directly or with ‘viewpoint shift’, a more flexible version of transposition. Property 4 seems to be instantiated more generally in the pragmatics of human and animal communication, as repetition can convey intensification and/or excitement (e.g. *Go, go, go!*). We further show experimentally that properties 1–3 are instantiated in some gestures understood by non-signers. Thus the waggle dance is a primitive form of a semantic system also found (through convergent evolution) in human language. It is remarkably ancient, at least 20 million years old according to phylogenetic reconstructions. While the horizontal dance (without transposition) is usually thought to be ancestral, a closer look at extant phylogenies suggests that the vertical dance (with transposition) might be more primitive, and furthermore that pre-adaptations guarantee that transposition might have been available from the start.

Key words: waggle dance of bees, iconicity, sign language, classifier predicates, animal semantics, evolutionary animal linguistics.

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I. INTRODUCTION

(1) The waggle dance

The waggle dance of bees is possibly the most studied and best understood system of animal communication. It is also one of the most striking. After locating a food source, a honey bee (*Apis* spp.) can signal (1) its distance through the duration of the waggle run, and (2) its direction through the orientation of the waggle run. In addition, (3) there are two broad types of dance: in bees with a horizontal nest, the dance is itself horizontal, and oriented towards the food source, whereas in bees with a vertical nest and dance, the latter requires transposition: the angle of the dance direction relative to ‘upwards’ is interpreted as the angle of the food direction relative to the sun (several bee species with a vertical dance can also dance horizontally, without transposition, which we return to in Section VI). Finally, and less clearly, (4) the number of waggle runs increases with food quality (TAnson Price & Grüter, 2015; Seeley, Mikheyev & Pagano, 2000; we come back below to the relationship between the waggle dance and the round dance).

In his pioneering work, von Frisch (e.g. von Frisch, 1967) called this system ‘symbolic’, but in contemporary terminology it is best characterized as iconic (e.g. Corballis, 1993, p. 138; Tuttle, 2014, p. 572; Ludden, 2015, p. 13). Informally, a sign is iconic if it denotes something by virtue of resembling it. More formally, a sign is iconic if there is a structure-preserving map between its

form and what it denotes (in other words: its denotation has the same structure as its form). A simple example in human language is: *The talk was loong, or loooong, or loooooong*: the duration of the vowel ‘resembles’ that of the talk. Here the structure-preserving map is simple: the longer the vowel, the longer the talk. By contrast, a sign is symbolic if it denotes by virtue of a convention (e.g. *cat* denotes felines, but there is nothing in the form of ‘cat’ that resembles or has the same structure as felines).

Informally, there is a structural resemblance between the form of the waggle dance and its meaning. For instance, the horizontal dance directly points towards the food source, just as the flight it should trigger (this resemblance is at the heart of analyses that treat the waggle dance as an intended flight; Menzel, 2019). More formally, there is a structure-preserving map between the form of the dance and its meaning. To put it roughly: the longer the run, the further the food; the greater the angle of the run (relative to the sun direction for a horizontal dance, or relative to upwards for a vertical dance), the greater the angle of the food direction (relative to the sun); and the more waggle runs, the better the food.

(2) Relation to human language

It has been claimed that this gradient iconic system bears little resemblance to human language, which is essentially

symbolic and discrete (e.g. Benveniste, 1953; Chomsky, 1975; Janda, 1978; Anderson, 2004). We argue that this verdict is mistaken and stems from an overly narrow view of human language. In numerous sign languages, a designated construction, the classifier predicate (or ‘classifier’ for short), displays a striking similarity to the waggle dance: both (1) its duration and (2) its direction can be interpreted, and furthermore (3) direction can be interpreted either directly or with ‘viewpoint shift’, a more flexible version of transposition. As for property 4 (greater number of repetitions for greater food quality), it seems to be instantiated more generally in the pragmatics of human and animal communication, as repetition can convey intensification and/or excitement (e.g. *Go, go, go!*). Thus the waggle dance is a less expressive version of a system also found in human language [no doubt through convergent evolution rather than common descent, in view of the phylogenetic distance between humans and bees, whose last common ancestor lived more than 600 million years ago (Earl, 2023; Kumar *et al.*, 2022)].

How old is the bee version of this semantic system, and what was its original form? The waggle dance has been determined to be at least 20 million years old using phylogenetic reconstruction methods (F'Anson Price & Grüter, 2015; see Section VI.1). The horizontal dance (without transposition) is usually thought to be ancestral, in part because it seems that transposition may be an elaboration on a simpler system. But a closer look at extant phylogenies suggests that the question is open: the vertical dance (with transposition) might have been present in the most recent common ancestor of extant dancing bees, and furthermore pre-adaptations might guarantee that transposition could have been available from the start.

(3) Structure

First, we summarize the four main properties of the waggle dance (Section II), and explain that properties 1–3 (direction, duration, transposition) are found in sign language classifiers (Section III), while property 4 (repetition) is a more general feature of spoken and sign language expressions (Section IV). We show experimentally that properties 1–3 can also be evidenced in non-signers’ understanding of gestures (Section V). Finally, we explain how the bee dance was determined to be at least 20 million years old, and why reconstruction methods make it relatively likely that its ancestral form involved transposition (viewpoint shift), a surprising result in view of commonly held assumptions (Section VI).

II. THE DANCE LANGUAGE AND ITS RELATION TO HUMAN LANGUAGE

(1) Properties of the waggle dance

Following von Frisch’s pioneering work (e.g. von Frisch, 1967), it was found that ‘the dance, performed by a honey bee upon returning to the colony having successfully located a food

source, offers information on the presence, odor, quality, direction, and distance of said food source, enabling nest-mates to exploit it (...). The direction information is conveyed through the orientation of the waggle run, whereas the distance information is expressed through the duration of the waggle run’ (F'Anson Price & Grüter, 2015, pp. 1–2). Distance is measured by optic flow, i.e. ‘the flow of retinal images experienced by the bee through its motion’ (Esch, 2012, p. 57; see also Esch *et al.*, 2001). In addition, ‘the higher the profitability of a particular source, the greater the number of waggle runs produced by a bee working this source when she returns to the hive’ (Seeley *et al.*, 2000, p. 813).

Depending on the bee species, the dance orientation that specifies the direction of the food source is interpreted in one of two ways. In some bee species, the part of the nest used for dancing is horizontal. Correspondingly, the dance, performed by crawling in the hive, is performed horizontally as well, and the waggle run points towards the food source. In other bee species, the dance area is vertical and the dance is therefore performed vertically; in that case, the angle of the dance relative to ‘upwards’ is interpreted as the angle of the food direction relative to the sun, as illustrated in Fig. 1.

In all cases, the dancer’s perspective is primary and the observer’s perspective plays no designated role, for two reasons. First, the observing bees initially surround the dancer from different positions, corresponding to diverse perspectives (there is no single ‘addressee perspective’, unlike in human language). Second, if the dance is successful, the observing bees end up following the dancing bee and thus adopting the same perspective.

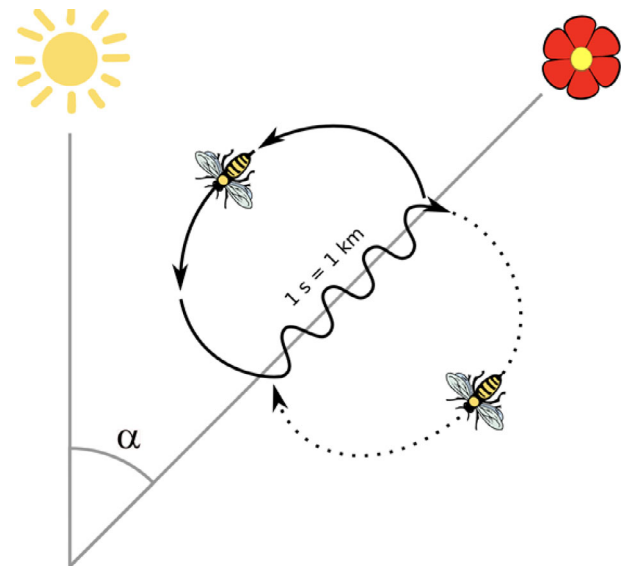


Fig. 1. Transposition in the vertical dance of bees. The angle of the waggle run relative to gravity is interpreted as the angle of the food direction relative to the direction of the sun. The duration of the waggle run is interpreted in terms of distance, here with 1 s corresponding to 1 km. Credit: https://commons.wikimedia.org/wiki/File:Bee_dance.svg.

The main dance types are illustrated in Fig. 2 (we follow the discussion of Schlenker *et al.*, 2025b). In Fig. 2A, the dance is horizontal, and is oriented towards the food source (the flowers). In Fig. 2B, the dance is vertical and in the open, in an upwards direction. This indicates that the food source is towards the sun from the bee's position. The dance in Fig. 2C is similar to that in Fig. 2B, with the difference that it is

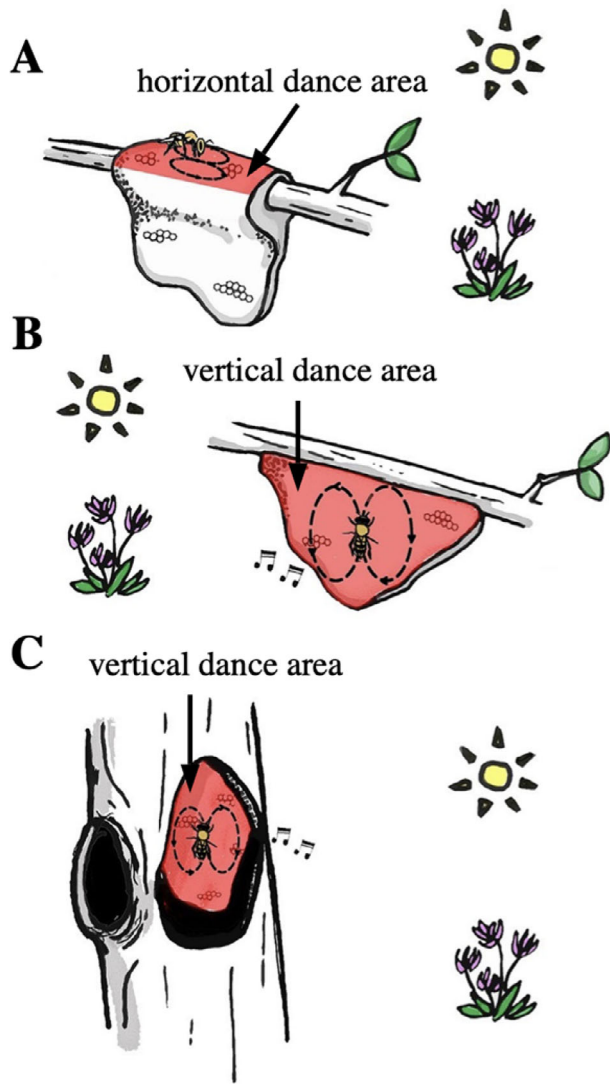


Fig. 2. Types of waggle dance (modified from l'Anson Price & Grüter, 2015). (A) Dwarf honey bees (*Apis florea*) perform dances on a horizontal surface in the direction of the food source. (B) Giant honey bees (*Apis dorsata*) perform dances on a vertical surface and orient dances with gravity and celestial cues. (C) Cavity-nesting honey bees (*Apis mellifera*) perform dances in darkness on a vertical surface. Dances are oriented with gravity and celestial cues. The giant honey bee and cavity nesting bees produce auditory cues when dancing. Bees in B and C are both dancing directly upwards, indicating that the food source is in the direction of the sun. Areas of the comb on which bees dance are indicated by an arrow (and appear in red in the online version).

performed by cavity-nesting bees, and thus in darkness. Here too, the dance is oriented upwards, indicating that the food source is oriented towards the sun. Observer bees 'touch the dancer directly with their antennae during the dance' (Grüter & Farina, 2009 p. 243), and thus obtain spatial information [in addition, the dancer 'produces airborne sounds, airflows and vibrations in the comb, as well as releasing chemicals', and the relative importance of different signal types is still being investigated (Grüter & Farina, 2009 p. 243; see also Michelsen, 2012)].

Remarkably, several bee species with a vertical dance and thus transposition (e.g. *Apis dorsata*, *Apis cerana*, *Apis mellifera*; see Section VI) can switch to a dance pointing towards the food source (without transposition) if the plane becomes horizontal. By contrast, *Apis florea*, which has a horizontal dance, does not adopt transposition when forced to dance vertically (Dyer, 1987).

It is useful to give names to the four properties of the waggle dance we have discussed, as shown in Table 1.

Repetition might have a different status from the other properties. Only rarely does a bee follow a dance from beginning to end, and thus follower bees do not know how long the target bee has already been dancing or will be dancing before it stops (Grüter & Farina, 2009; Biesmeijer & Seeley, 2005). As a result, they do not know how many waggles the dancer performs, and thus individual follower bees might not interpret the number of waggle runs (in fact, follower bees may directly assess nectar quality when they receive small samples from the dancer during short dance breaks). On the other hand, it might be that follower bees *as a group* indirectly interpret this information because the more runs there are, the more bees will follow the dance and might thus be convinced to initiate flight towards the indicated food source.

(2) Waggle dance versus round dance

As summarized by Gardner, Seeley & Calderone (2008), throughout his career von Frisch consistently distinguished the waggle dance from another dance: the round dance

Table 1. Properties of the waggle dance.

Property 1: Duration	The duration of the waggle run provides information about the distance of the food source.
Property 2: Direction	The direction of the waggle run provides information about the direction in which the food source is found.
Property 3: Transposition	In the vertical dance, dance direction is interpreted relative to a shifted viewpoint: the angle of the dance direction relative to 'upwards' provides information about the angle of the food direction relative to the sun.
Property 4: Repetition	The number of waggle runs provides information about the quality of the food source.

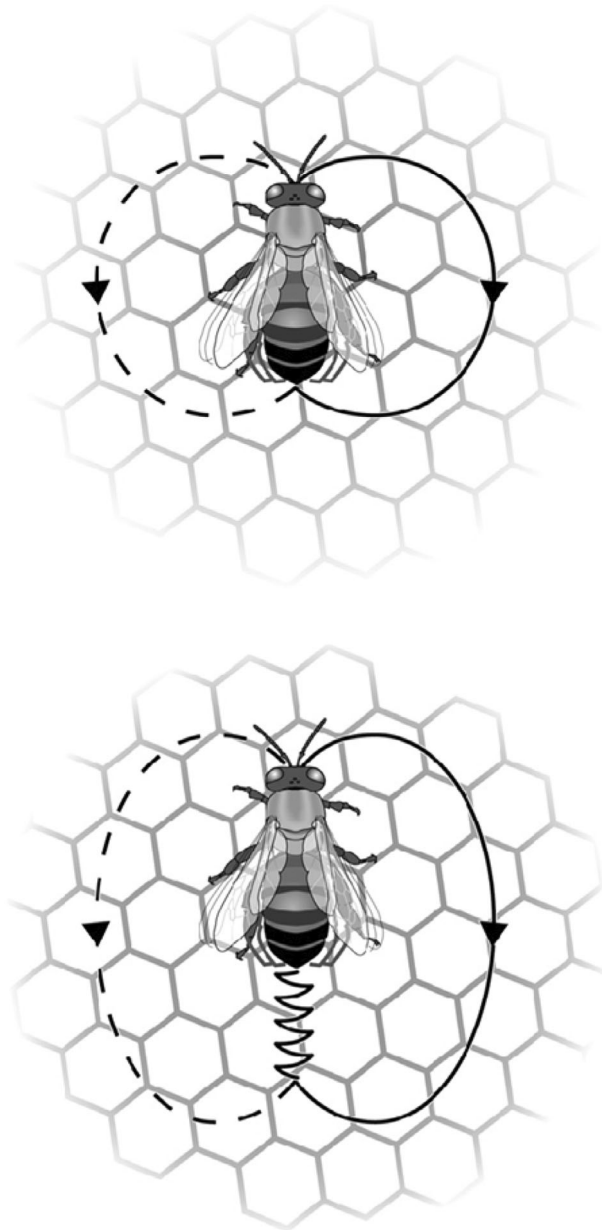


Fig. 3. Round dance and waggle dance (Gardner *et al.*, 2008, p. 1292). ‘Top: the round dance, wherein the dancing bee completes rapid circular manoeuvres, each one starting with a brief wagging of the abdomen, then a turn to the left or right, and finally a circle back to the starting point. Bottom: the waggle dance, wherein the dancing bee completes elongate manoeuvres, each one starting with a conspicuous and prolonged period of abdomen wagging, then a turn to the left or right, and finally a walk back to the starting point.’

(Fig. 3). The view was that in producing the round dance, ‘a bee steps excitedly in a circle, then suddenly turns to reverse her direction of travel, circles around again before reversing again, and so on. In producing the waggle dance, a bee steps straight ahead for a short distance, then turns to travel back to her starting point, again walks through a straight length,

then makes a turn in the opposite direction, and so on in regular alternation. A vigorous wagging of the body gives special emphasis to the straight part of the waggle dance, so it is often called the “waggle phase”.’ (Gardner *et al.*, 2008, p. 1291). The general idea in von Frisch’s work was that the round dance was used to advertise a food source near the hive (up to about 50 m), without orientation information, whereas the waggle dance provided information (including orientation information) about food sources further away (e.g. von Frisch, 1967, p. 62).

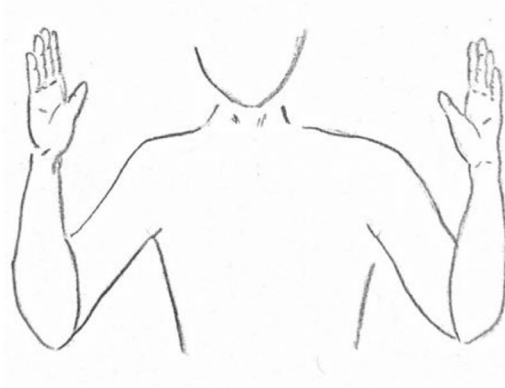
Contrary to von Frisch’s view, Gardner *et al.* (2008, p. 1297) show that there is no categorical distinction between the round dance and the waggle dance: ‘the round and waggle dances are merely two ends of a continuum; “adjustable waggle dance” is sufficient. Distance and direction are encoded using the same mechanisms in both dances, and the predictability of dance behaviour gradually increases as the food-source distance increases.’ Still, one might conceptualize the situation as follows. The dance (whether round or wagging) indicates that food has been found. When the food is nearby (up to about 50 m from the hive), the unmodified round dance must be used. When the food is further away, modifications of the dance involving the waggle dance become obligatory. One could thus take the wagging version to be an iconic modification of the dance, but when the food is far enough, it is crucially an obligatory modification; this case thus differs from that of English *loong*, where the iconic lengthening of the vowel is always optional (‘long’ by itself can be semantically applied to multiple degrees of length).

(3) The dance language as an iconic system

As mentioned in Section I.1, a sign is iconic if it denotes something by virtue of resembling it. Formally, a sign is iconic if its form has the same structure as what it denotes, or in other words if there is a structure-preserving map between the two (e.g. Schlenker, Lamberton & Santoro, 2013; Emmorey, 2014). In the case of *long*, an ordering of realizations of the vowel length is mapped to an ordering of (talk) durations. A gestural example is given in Fig. 4, where the larger the gesture, the greater the fish is supposed to be.

Importantly, to say that a sign is ‘iconic’ is not to say that *everything* about the sign is iconic (see for instance Greenberg 2023). The term *long* is conventional, but one can iconically lengthen the vowel. Even in the gestural example of Fig. 4, the hands do not resemble anything pertaining to the fish, although the distance between the hands resembles (or can be mapped to) the length of the fish. We will see in Section III that a stereotypical case of iconicity in sign language involves conventional signs whose position and movement can be modulated in highly iconic ways.

Both informally and formally, the waggle dance qualifies as an iconic system, although it too has fixed (non-iconic) elements. From von Frisch (1967, p. 324) to Menzel (2019), a key idea has been that the waggle dance incorporates elements of an intended flight and thus partly resembles one. This is particularly clear for the horizontal dance, which



‘I caught a fish like this’

Fig. 4. An iconic gesture in a sentence. Picture by M. Bonnet, reprinted under Creative Commons CC BY 4.0.

points towards the food source. von Frisch (1967) further interpreted tail-wagging as ‘as repeated starts to take off’ (p. 324), and certainly dance duration ‘resembles’ the duration of the flight needed to reach the food (or more precisely: the optic flow during that flight). For his part, Menzel (2019, p. 2) argued that, for the follower, ‘the waggle run mirrors its next outbound flight, a performance that will follow when she leaves the hive’. Formally, there is a structure-preserving map between three properties of the dance and its meaning in terms of movement, as stated at the end of Section I.1: the longer the run, the further the food; the greater the angle of the run (relative to the sun direction for a horizontal dance, or relative to upwards for a vertical dance), the greater the angle of the food direction (relative to the sun); and the more waggle runs, the better the food. Still, the waggle dance has fixed elements that are not interpreted, notably the non-wagging part of the movement represented in property 4; it is thus an iconic system with a categorical component.

What is admittedly confusing is that von Frisch himself applied the term ‘symbolic’ to the waggle dance (e.g. von Frisch, 1954, 1967). But von Frisch used the term ‘symbolic’ in a very broad sense, as made explicit in von Frisch (1954, p. 6): ‘Symbols are signs for something else to which they stand in a certain relation’. On the other hand, in his foreword to the second printing of von Frisch (1967), Seeley put the point more radically: ‘the bee’s communication system is symbolic rather than iconic, for the signal used has no particular resemblance to the action it represents.’

Menzel’s (2019) analysis in terms of intended flight was in the opposite direction. But the key is that ‘resemblance’ is not a well-defined notion, which is why formal accounts prefer to define iconicity in terms of a structure-preserving map. On this view, the waggle dance is clearly iconic. For other authors that treat the waggle dance as iconic, see for instance Corballis (1993, p. 138), Tuttle (2014, p. 572) and Ludden (2015, p. 13).

(4) The ‘dance language’ debate

von Frisch promoted the term ‘dance language’ (including in the title of his influential book *The Dance Language and*

Orientation of Bees; von Frisch, 1967), which naturally raised the question whether the system described above genuinely counts as a language. The first question was whether there is genuine communication: does the dance just *reflect* information about food location or does it *convey* it, in the sense that follower bees use this information (rather than something else, e.g. food odour) to locate the source? Decades of experiments have mostly vindicated von Frisch’s insights: the dance language is a communication system (Riley *et al.*, 2005; see also A1 in Appendix S1 in the online Supporting Information).

The second question was whether this communication system is a language. One version of the debate is purely terminological: can the term ‘language’ be applied to an iconic and gradient system rather than to the symbolic and discrete linguistic systems we are used to? As for all terminological questions, there is no easy answer [see for instance Schlenker *et al.* (2016) for a very broad use of the term ‘language’ in animal linguistics, from which the answer to the terminological question would be positive]. But behind this lurks a more substantive question: does the bee communication system (henceforth the ‘dance language’) have any interesting properties in common with human language?

Early on, the great linguist Emile Benveniste argued in the negative, for two main reasons (Benveniste, 1953). First, ‘there can be no real language without the exercise of voice’ (p. 5). Second, the content of a human linguistic expression radically differs from that of the bee dance because ‘it is impossible to resolve this content [= that of the bee dance] into its constituent “morphemes” and to make each morpheme correspond to an element of what has been enounced’ (p. 6).

The first reason was later shown to be spectacularly wrong. Human language exists in two modalities, the vocal and the visual one, and sign languages and spoken languages share key formal and neurological properties [e.g. see Sandler & Lillo-Martin (2006) for a view from formal linguistics, and MacSweeney *et al.* (2008) for a view from neuroscience].

Still, in a well-documented book, the linguist Stephen Anderson developed a version of the second objection (Anderson, 2004), which is certainly the dominant view in linguistics. It is also

hinted at by Chomsky (1975) (see also A2 in Appendix S1). For Anderson, while sophisticated and rather expressive, the dance language is entirely different from human language because it ‘has a property that human languages do not have: continuous variation along its component dimensions. Human languages have discrete, not continuous, vocabularies (whatever a “continuous” vocabulary might be). Words are simply distinct from one another, rather than one shading gradually into another’ (Anderson, 2004, p. 80). Needless to say, Anderson in no way implied that human language only exists in the vocal modality; and in fact, sign languages have discrete vocabularies just like spoken languages, which dovetails with Anderson’s argument (we will see that *besides* their discrete vocabularies, sign languages also have gradient, continuous constructions).

Anderson was cautious to temper his verdict, however. ‘Having said this, I must immediately point out that the way we use language in concrete acts of speaking involves more than the contributions of vocabulary and grammar. One important additional system is known as paralanguage: the gestural and emotional accompaniments to speaking, such as loudness and tone of voice, pitch (to some extent), rate of speech. These aspects of speaking we can vary continuously, to indicate, for example, an unlimited number of degrees of excitement by correspondingly varied loudness or pitch.’ (Anderson, 2004, p. 81). The examples of iconicity cited above – *the talk was looong; I caught a fish like this [with a gesture]* – might be taken to fall under Anderson’s paralanguage.

As we will now see, Anderson’s verdict was still in error because it failed to consider constructions of sign language that are not paralinguistic but display striking similarities with the dance language of bees.

III. SIGN LANGUAGE ICONIC CONSTRUCTIONS: DIRECTION, DURATION AND TRANSPOSITION

(1) Classifier predicates

Sign languages notoriously have the same type of grammatical and semantic resources as spoken languages (e.g. Sandler &

Lillo-Martin, 2006), and thus they have a discrete and conventional vocabulary just like spoken languages do. But in addition, they have a distinguished category of expressions, classifier predicates (‘classifiers’ for short), which are used in iconic ways. Specifically, they (i) have a lexically specified form, but (ii) their position in signing space, their orientation and their movement (if there is one) are unconstrained, and interpreted iconically [classifiers ‘are reported to occur in almost all sign languages researched to date’ (Zwitzerlood, 2012, p. 158); here we follow Schlenker & Lamberton (2024) and Schlenker *et al.* (2024)].

A textbook example appears in Fig. 5A, with the rough meaning in Fig. 5B: a vehicle classifier represents a car, and the movement of the predicate in signing space iconically depicts the movement of the car.

The gradient and iconic character of the information conveyed was displayed in an experiment by Emmorey & Herzig (2003). They studied a construction involving a (static) classifier representing a small object (a sticker) relative to a handshape representing a flat object (a bar). Deaf signers were asked to provide a geometric representation of the scene. As the classifier’s position was gradually modified relative to the flat object handshape, so was the geometric representation of the scene: the signs were interpreted iconically [for dynamic classifiers, see for instance Zucchi (2017) and Schlenker & Lamberton (2024)].

In Fig. 5A, the direction of the classifier movement can be interpreted (a car drove in the direction displayed), and the duration and extent of the movement can be too: a movement with a longer path can be interpreted as a greater displacement of the car; and keeping the path length constant, greater duration might signify a movement that takes more time. Importantly, classifiers typically give rise to iconic interpretations. For instance, Schlenker & Lamberton (2024) discuss minimal pairs involving a standard nominal version of the sign for *plane* [with the duplication characteristic of ASL (American Sign Language) nouns], and a classifier version with the same meaning (without the duplication). While iconic interpretation is an option for the nominal version, it is strongly preferred or obligatory for the classifier version. For this reason, it might not make much intuitive sense to

(A) CAR CL-vehicle-DRIVE-BY



(B) ‘A car drove by *like this*’, where the information contributed by *like this* is produced by the movement of the classifier predicate in signing space

Fig. 5. Example of a classifier in ASL, with an iconic interpretation of its movement. (A) The ASL sign (cited and illustrated from Valli & Lucas, 2000). (B) The approximate meaning (after Zucchi, 2011).

treat the iconic component of classifiers as paralinguistic – it lies at the core of sign language. How ‘grammatical’ or ‘linguistic’ classifiers are taken to be depends on one’s definition of grammar and language; see for instance Zucchi (2017) for a summary of the debate.

The case of the vehicle classifier illustrated in Fig. 5 involves iconic interpretation of the entire path and duration. By contrast, in the waggle dance as standardly described, the direction and duration are interpreted, but not the path *per se* (e.g. Grüter & Farina, 2009; see also A3 in Appendix S1). Still, one can find different realizations of classifiers in which only direction and duration are interpreted.

(2) Direction and duration

Signers can emulate the behaviour of the waggle dance by using classifiers to encode direction and duration. This will now be illustrated with an example from ASL. Appendix S2 discusses in detail multiple additional examples involving diverse classifiers. In line with standard methods in sign language semantics, two kinds of data were obtained when the videos were played back to the signer (a Deaf native signer of ASL, and a co-author of this article): acceptability of the sentences; and difference inferences drawn from them. In a second step, a subset of the data were informally checked with another Deaf native signer of ASL (also a co-author, and the brother of the first signer). Judgments are reflected by the translations. See Appendix S2 for further details about the method and results.

For simplicity, we consider a case in which the path has constant length and only the duration varies. For even greater clarity, we focus on a classifier that represents a small animate entity, e.g. a wasp or bee. We have added some images to the transcriptions to illustrate sample realizations of this classifier.

The example in Fig. 6 involves a game in which the signer must convey as precisely as possible what a bee he released just did. But the signer can use just one word to convey the information, which makes it natural to use a classifier, as it can convey rich iconic information (see also A4 in Appendix S1). Classifier direction is very naturally used to encode movement direction in all cases. The interpretation of duration *per se* is harder, and made possible here by the ‘one word’ rule of the game as specified (see Appendix S2 for details; our main consultant was far more liberal than our second consultant in the use of pure duration). Duration would normally be accompanied by other means of intensification (notably facial expressions), which were not present in our elicited sentences because we were trying to assess the interpretive role of duration on its own.

All target sentences start with an ASL sequence that means: *What the bee did was ...*, followed by different realizations of the classifier in different examples. Two parameters were investigated: the direction of the movement, towards the signer’s right or the signer’s left (examples a–c versus d–f); and the duration of the movement: short (a, d), medium (b, e), long (c, f). In all cases, the classifier path was held

roughly constant. The goal was to emulate two properties of the horizontal waggle dance, where direction and duration are interpreted.

In this case, the classifier direction corresponds to the movement of the bee the signer had released, seen from the signer’s perspective. This is so because a standard rule across sign languages (e.g. Pyers, Perniss & Emmorey, 2015) is that classifiers represent objects from the signer’s perspective (in addition, to the extent that space is shared between the signer and addressee in the present case, the direction has to match the direction of the bee flight). This correspondence is represented in Fig. 7 (we assume for simplicity that the classifier is at a 45° angle relative to the signer’s ‘forward’ direction).

The examples are robust to multiple changes, as discussed in Appendix S2. Let us mention three of these. First, classifiers that have nothing to do with bees can be used, such as the vehicle classifier represented in Fig. 5A, or a classifier representing a person walking, shown in Fig. 8.

Second, with some classifiers (including the small animate entity classifier seen in Figs 6 and 7), the forward hand movement can be eliminated; a trembling stationary movement suffices to indicate that the denoted object moved, and then represents the duration of the object’s movement, and thus indirectly distance. It is also possible to vary both path length and path duration to represent different object displacements.


Third, further constructions besides classifiers can be used in a similar way. On the one hand, ASL has a category of spatial verbs, for instance verbs meaning *go to*, *move to*, *run to*, etc. They involve a manual movement towards a location of signing space that corresponds to their grammatical object (e.g. *run to place x*, where *place x* is the grammatical object of *run to*), and they can often be modulated so that the direction in which they point indicates the direction of the denoted movement. In examples involving the verb *RUN*, depending on whether the sign targets the right or the left, the running is understood to be towards the right or left from the relevant perspective (e.g. the signer’s perspective). The sign duration may optionally provide information about the duration of the run. On the other hand, a verb that involves the signer’s upper body and no manual displacement, *JOG* (which iconically resembles a person jogging), can be used with similar effects. The direction of the signer’s body and the duration of the sign provide information about the direction and duration of the denoted movement.

In sum, there are clear examples in which sign direction and duration can be modulated and interpreted gradiently, roughly as in the horizontal waggle dance: the sign direction provides information about the direction of the movement, and (in the game context we specified) the sign duration provides information about the duration of the movement. Importantly, there is a difference relative to the waggle dance: the latter’s duration provides absolute information about food distance, to the point that researchers can use the former as a proxy for the latter (Schürch *et al.*, 2019). In ASL, by contrast, only *relative* duration can be interpreted, and it is thus in contrast with each other that the sentences yield clear ordinal inferences in this respect.

Context [signed in ASL as part of the target video]: The signer and addressee are on the same team. The signer recently released a bee and saw where it went to reach its hive. The addressee did not see this. The signer can convey the information, but using just one word. The signer and addressee know that there are several possible hives, distributed at different distances from the release point. Some are very close (5 m), some are quite far (200 m), and others in between.


BEE DO WHAT?

‘What the bee did was

a. FLY-constant-displacement-cl-right-short_duration_ 
fly to the right for a little time.’

b. FLY-constant-displacement-cl-right-medium_duration
fly to the right for quite a while.’

c. FLY-constant-displacement-cl-right-long_duration
fly to the right for a very long time.’

d. FLY-constant-displacement-cl-left-short_duration_ 
fly to the left for a little time.’

e. FLY-constant-displacement-cl-left-medium_duration
fly to the left for quite a while.’

f. FLY-constant-displacement-cl-left-long_duration
fly to the left for a very long time.’

(ASL 37, 3082)

Fig. 6. Target ASL sentences in the context of a game in which the signer must convey as precisely as possible what a bee just did. In line with standard transcriptions for sign language, the word-for-word English translation is given in capital letters. Here *FLY-constant-displacement-cl* transcribes a flying classifier (hence the suffix *-cl*) involving a constant displacement. The direction of the displacement and its duration are encoded after *-cl*. For instance, FLY-constant-displacement-cl-right-short_duration involves a short movement towards the signer’s right. See Appendix S2 for further transcription conventions. Video (target sentences only): <https://youtu.be/VxD7BX1b724>, Video (with the context): <https://youtu.be/npvmIFsFfVA>.

In other respects, classifiers are undoubtedly far more expressive than the waggle dance, as the detailed path as well as changes of speed can be represented, among other features.

(3) Adding simulation

Most of the examples discussed so far differ from the waggle dance in that direction and distance are conveyed by hand rather than body movement. As briefly mentioned above, there is an exception, however: the verb *JOG* involves the upper part of the body, as shown in Fig. 9A, and its direction and the duration of the sign indicate the direction and duration of the running.

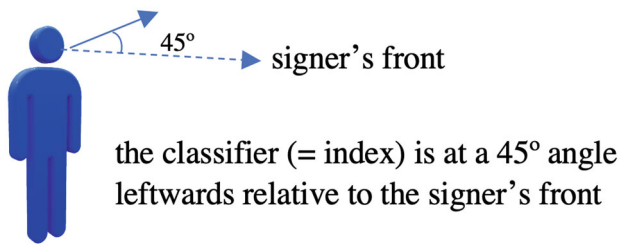
In the case of *JOG*, the fact that the sign is realized with the whole upper body is just a property of its form. But in addition, there is a designated construction that comes close to simulation. It is called Role Shift, and it has two distinct uses: one involves reported speech or thoughts; the other involves action reports. In Role Shift, the signer typically

shifts their body and eyegaze to adopt the perspective of another character (see also A5 in Appendix S1). Our main data can be replicated with Role Shift used to report an action, notably with *JOG*, illustrated in Fig. 9B in its version with Role Shift, involving in particular eyegaze shift away from the addressee. Role Shift can be applied to manual constructions as well, such as the classifier representing a person walking. It appeared in Fig. 8A without Role Shift, and is given in Fig. 10 in a version with Role Shift, which involves body rotation and eyegaze shift. In the version of *JOG* with Role Shift, we have a rather striking case in which the signer’s entire upper body serves to simulate a person running. This partial simulation is reminiscent of the idea that the waggle dance represents an intended flight, as argued by Menzel (2019).

(4) Adding transposition

The properties of ASL discussed so far make it possible to replicate the gradient interpretation of the direction and

(A) FLY classifier



(B) Interpretation without transposition: the sign direction directly indicates the bee movement direction

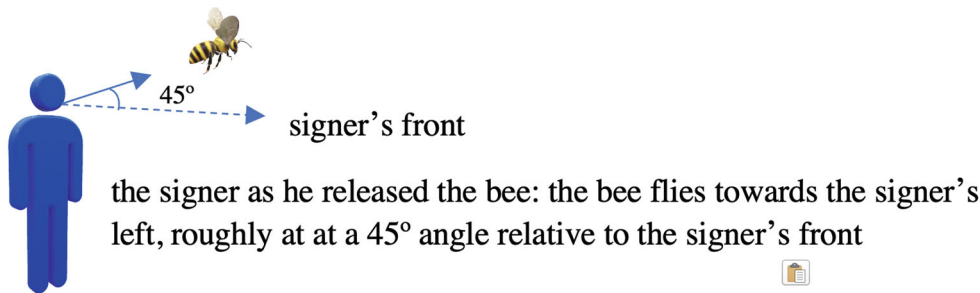


Fig. 7. Interpretation of the FLY classifier in Fig. 6d–f, without viewpoint shift.



Fig. 8. Examples of a classifier representing a person walking. (A) Classifier representing a person walking towards the right. (B) Classifier representing a person walking towards the left.



Fig. 9. (A) JOG without Role Shift (no eyegaze shift). (B) JOG with Role Shift (eyegaze shift).

duration of the horizontal waggle dance. But the vertical dance crucially involves transposition. To reiterate, an observer that sees a bee dancing vertically must take the angle of the dance direction relative to the vertical to be interpreted as the angle of the food direction relative to the sun.

This too can be found in sign language constructions, most definitely, and in a highly generalized form. Depending on the context, the movement of a classifier can be interpreted from the signer's viewpoint, or from a salient viewpoint given by the context. In the former case (signer's viewpoint), the

classifier moves in the same direction as the depicted object. In the latter case (salient viewpoint), the classifier's movement relative to the signer is interpreted as the depicted object's movement relative to a salient viewpoint. If the salient viewpoint is someone looking towards the sun, the angle of the classifier movement relative to the signer's forward direction corresponds to the angle of the object movement relative to the sun's direction. But there are many more viewpoints that can be contextually salient. Thus this is a more expressive mechanism than is found in the waggle dance because

transposition is not limited to ‘upwards corresponds to the direction of the sun’: any salient viewpoint will do.

The general availability of viewpoint shift in sign language is well established (e.g. Schlenker & Lamberton, 2024), and it is determined by contextual considerations. It can be illustrated in the case of the small animate entity classifier by changing the context, as in Fig. 11. The signer and interlocutor are now in a room and discuss what happened yesterday when a third person, Ann, released a bee in the signer’s presence. The same classifier as in our earlier examples will now be taken to indicate iconically where the bee went *from Ann’s viewpoint*.

The interpretations without viewpoint shift (= without transposition) were illustrated in Fig. 7A,B. With viewpoint shift/transposition, the direction of the classifier movement remains the same as in Fig. 7A (repeated as Fig. 12A), at a 45° leftward angle relative to the signer’s front. But this is now interpreted from Ann’s rather than from the signer’s perspective, as seen in Fig. 12B.

This is the same type of operation needed to interpret a vertical waggle dance. To highlight the similarity, we can think of someone (the equivalent of the signer) looking upwards towards the vertical, as in Fig. 13A below. The waggle run (the equivalent of the classifier) is at a 45° angle relative to the vertical and thus relative to this person’s left. To obtain the direction of the food, we must imagine a person



Fig. 10. Classifier representing a person walking towards the right, with Role Shift: the signer rotates his body and shifts his eyegaze towards the right.

Alternative context for Fig. 6: The signer and addressee are on the same team, **and they are now in a room. Yesterday another person, Ann, released a bee**, and the signer saw where it went to reach its hive. The addressee did not see this. The signer can convey the information, but using just one word. The signer and addressee know that there are several possible hives, distributed at different distances from the release point. Some are very close (5 m), some are quite far (200 m), and others in between.

Fig. 11. Alternative context for Fig. 6, triggering a viewpoint shift: the signer adopts Ann’s viewpoint.

looking towards the sun: the food direction is at a 45° angle towards this person’s left, as seen in Fig. 13B. Transposition in the vertical dance is an inflexible instance of viewpoint shift, which in sign language allows for multiple salient viewpoints, not just that of someone facing the sun. As shown in Appendix S2, viewpoint shift can similarly be applied to all the example types mentioned above.

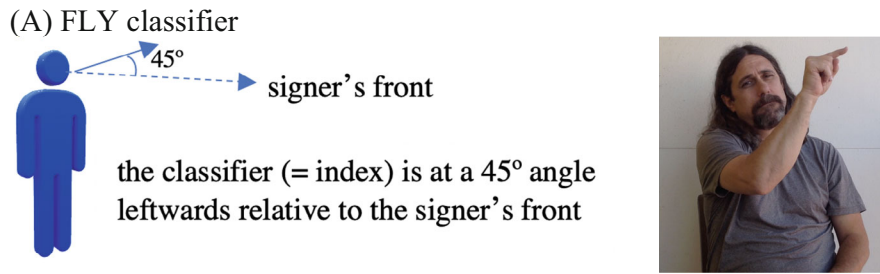
IV. SIGN LANGUAGE AND SPOKEN LANGUAGE: REPETITION

(1) Repetition to express intensification or urgency

The final key property of the waggle dance is Repetition (= property 4), whereby larger numbers of iterations encode higher food quality. Here it is not specifically classifier predicates that offer a counterpart of the waggle dance, but more generally human language and probably many other communication systems: repetition can serve to convey intensification of a property, as in Fig. 14, or of an order, as in Fig. 15 (see also A6 in Appendix S1).

Unsurprisingly, the same effects are found in ASL, as seen in Appendix S2: the ASL predicates *RICH*, *STOP*, and *LEAVE* can be iterated twice or three times to convey different degrees of intensification/urgency. The same operation can be applied to a classifier representing a helicopter taking off, illustrated in Fig. 16. In a war situation in which the signer is in a helicopter piloted by the addressee, two or three iterations can be interpreted to mean that the pilot should urgently take off. Our second consultant agreed with our main consultant on *STOP*, but for the other cases he would have realized the repetitions differently and/or with intensificational facial expressions (see Appendix S2).

The use of repetition to intensify an order comes close to the use of repetitions of the waggle dance to convey quality: the better the food, the more important presumably it is to collect it. This function of repetition in human language and arguably in bees might be part of more general animal code, by which more urgent events are expressed with greater calling rates (in other words, with more repetitions per time unit). An increased call rate in response to heightened urgency has been observed in the alarm calls of phylogenetically diverse species [e.g. birds (Templeton, Greene & Davis, 2005); mammals (McRae, 2020; Murphy, Lea & Zuberbühler, 2013; Lemasson *et al.*, 2010)]. Urgency levels have been assessed though varying



(B) Interpretation with transposition: the sign's direction relative to the signer indicates the direction of the bee movement relative to Ann's viewpoint

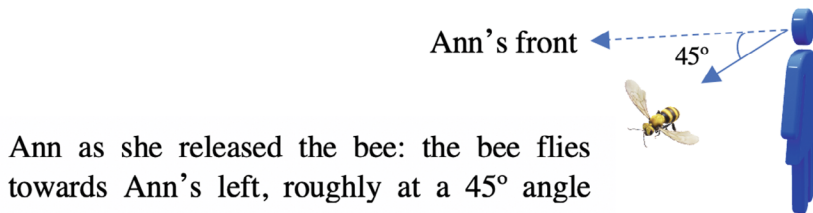
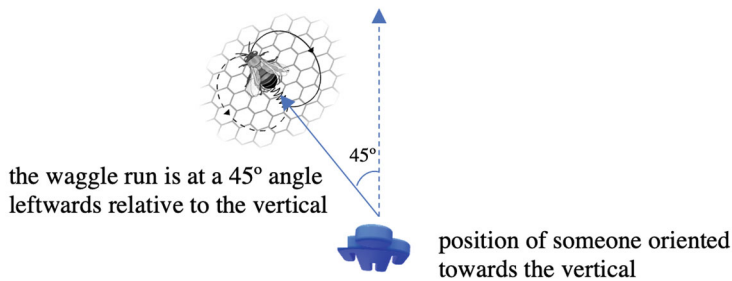


Fig. 12. Interpretation of the FLY classifier in Fig. 6d–f, with viewpoint shift: the signer adopts Ann's viewpoint.

(A) Waggle dance



(B) Interpretation with transposition: the waggle run's direction relative to the vertical indicates the food direction relative to the viewpoint of someone facing the sun

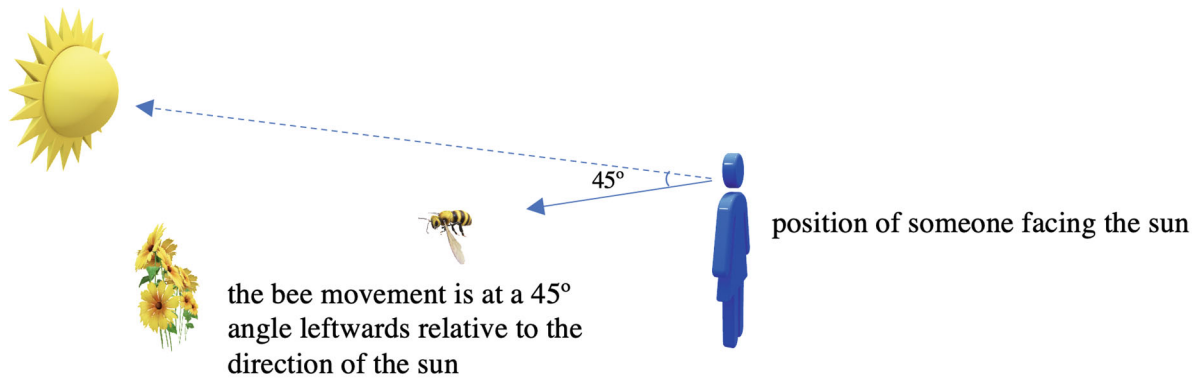


Fig. 13. Interpretation of the vertical waggle dance with transposition.

predator sizes (Malan, Seoraj-Pillai & Du Plessis, 2009; Courter & Ritchison, 2010; Dahl & Ritchison, 2018), distance to the threat (Leavesley & Magrath, 2005; Kryštofková, Haas & Exnerová, 2011; Dutour, Suzuki & Wheatcroft, 2020), or even orientation of the predator (Book & Freeberg, 2015).

Let us add that if the effect of repetitions does not affect bees as individuals but as a group (the more repetitions, the more bees get the signal), human counterparts can easily be found as well. Someone who cries ‘fire’ once will only affect whoever heard the message; someone who keeps crying ‘fire’ for 15 min might have a much greater effect owing to the increased size of their audience.

(2) Taking stock

We saw in Section III that duration, direction and transposition are properties of the waggle dance that are also found in ASL iconic constructions. We have also argued that repetition to intensify a property or an order is found more generally in spoken and sign language, including classifiers.

These similarities should not obscure some important differences. (i) Sign language classifiers have a much richer semantics than the waggle dance, as they can recreate details of the path and manner of movement of an object, not just its direction and length. Similarly, viewpoint shift is a far more powerful (and context-dependent) operation in classifiers than transposition in the waggle dance. (ii) There are two differences in the interpretation of duration. First, in sign language iconic constructions, duration seems to convey information about the duration of the denoted action, and only indirectly about the distance. In the bee dance, waggle duration is mapped to distance. Second, in sign language iconic constructions, duration differences are only interpreted relatively, whereas a given bee will translate duration into absolute distance [or rather optic flow (Esch *et al.*, 2001; Esch, 2012)], an extraordinary property of the waggle dance not shared by our human examples.

- a. I am rich!
- b. I am rich, rich, rich!
=> I am very rich

Fig. 14. Example of how repetition can convey intensification of a property in English.

- a. Stop
- b. Stop! Stop! Stop!
=> you must urgently stop

- a. Go!
- b. Go! go! go!
=> you must urgently go

Fig. 15. Examples of how repetition can convey intensification of an order in English.

V. ICONICITY IN GESTURES

(1) Classifier predicates and gestures

Owing to their free movement and iconicity, classifiers have sometimes been partly assimilated to a gestural component of sign language (e.g. Liddell, 2003a,b; Schembri, Jones & Burnham, 2005; Zucchi, 2011, 2017, 2018; Davidson, 2015; see also A7 in Appendix S1). In fact, the viewpoint dependency of classifiers (in the more general form discussed in the literature) was argued to extend to certain kinds of gestures (Schlenker & Lamberton, 2024; see also A8 in Appendix S1). This assimilation is at most partial because classifiers differ from gestures in having a conventional lexical form: for instance, the vehicle classifier illustrated in Fig. 5A is a word of the ASL lexicon and does not resemble a vehicle. For this reason, it is not justified to treat classifiers as belonging to the ‘paralinguistic’ component of language, to use Anderson’s (2004) terms. It should be added that, unlike the most common gestures (co-speech gestures), which merely accompany spoken words and are in this sense grammatically optional, classifier predicates cannot normally be omitted from a sentence without making it ungrammatical. More importantly, terminology aside, it is clear that sign language has both a discrete symbolic component and a gradient iconic component, with much of interest taking place at their intersection.

In sum, while Benveniste (1953) and Anderson (2004) were right to highlight the striking differences between the waggle dance and the discrete symbolic component of human language, there are equally striking resemblances between the waggle dance and the iconic and gradient components of human language, most clearly instantiated in sign language classifiers.

Still, owing in part to the partial resemblance between sign language classifiers and some spoken language gestures, recent research has argued that gestures should be



Fig. 16. A classifier representing a helicopter taking off (ASL 37, 2950d).

reintegrated as essential components of linguistic studies. In an influential programmatic article, Goldin-Meadow & Brentari (2017) argued that sign language with iconicity should be compared to spoken language with gestures rather than to spoken language alone, a view that is increasingly accepted in sign language and gesture studies alike.

One important difference requires mentioning, however. As alluded to in our discussion of Fig. 6, in sign language the signer's egocentric perspective is primary, in the following sense: when iconically depicting a scene he witnessed but the addressee did not (so that space is not shared), (i) a signer places objects as he sees them, and (ii) the addressee reconstructs the scene from the signer's perspective (Pyers *et al.*, 2015). Correspondingly, in Fig. 6d–f, the small animate entity classifier moving towards the signer's left indicates that the bee moved in that direction from the signer's perspective. Gesturers tend to also adopt an egocentric perspective in production, but addressees (i.e. perceivers) need not adopt the gesturer's perspective, which may lead to misunderstandings (Pyers *et al.*, 2015). This difference must be neutralized in order to compare gestures to signs. We will do so by creating situations in which the gesturer and addressee are oriented in the same direction, both facing the same scene (specifically, watching the same show).

(2) Direction, duration and transposition in gestures

(a) Experimental method

Leaving aside repetition, which is a more general property of sign and spoken language constructions, we might expect that direction, duration and transposition can be found in the iconic gestures of hearing non-signers. This is indeed the case. We will now show using an experiment that three key properties of the waggle dance (direction, duration, transposition) can be replicated in certain manual gestures.

The experimental context involves a drone competition in which the audience is asked to remain silent, so that communication among audience members has to occur by silent gestures. On the stage, there is a drone pilot, Anne, who can aim for one of six targets, as shown in Fig. 17. An audience member is depicted, either facing in the same direction as Anne (Fig. 17A), or facing in a different direction, rotated by 90° either clockwise (Fig. 17B) or counterclockwise (thus totalling three direction options). The audience member is communicating information to their neighbour, who is watching the same show and is thus oriented in the same direction (this serves to neutralize potential differences between gestures and signs regarding the way addressees interpret depictions).

The scene was designed with the following intention. In the first case (Fig. 17A), the gesturer should depict the drone pilot's action without transposition. For instance, if the gesturer performs a long forward hand movement in the centre, this should indicate that Anne should fly her drone upwards in the figure, towards the highest target in the centre. In the second case (Fig. 17B), in view of Anne's orientation, which is orthogonal to the gesturer's, the gesturer's depiction is

intended to be interpreted with transposition, adopting Anne's viewpoint. So if the gesturer performs a long forward hand movement in the centre, this should indicate that Anne should fly her drone rightwards in the figure, towards the rightmost target in the centre.

Participants saw the following context description: *The public is asked to remain silent, for the players' concentration. But someone nonetheless asks their neighbour: 'Where does Anne have to fly her drone?' The man shown in the bottom video (an avatar) provides a silent answer in gestures, using his hand to represent Anne's drone. The participant's task was to click on the target towards which, according to the gesturer, Anne should fly her drone. In other words, the participants' task was to interpret the gesture as Anne's neighbour would.*

Three parameters are modulated in the experiment: the direction of movement, as illustrated in Fig. 18 (see also A9 in Appendix S1); the duration of the movement; and the audience member's orientation relative to that of the drone pilot, as already seen in Fig. 17. The gesture was performed by an avatar, with the result that orientation and duration are perfectly controlled from one condition to the next (this would have been harder to achieve with a human model).

The last parameter (the avatar's orientation relative to the drone pilot) served to test transposition/viewpoint shift. In Fig. 17A, the avatar's gesture is interpreted without transposition as directly pointing towards the relevant target [for Fig. 18, forward (A) or forward–rightward (B) from Anne's and the gesturer's viewpoint]. In Fig. 17B, transposition is needed: the avatar has a different orientation from Anne, and thus its gestures only make sense if Anne's viewpoint is adopted to interpret them (with mental rotation).

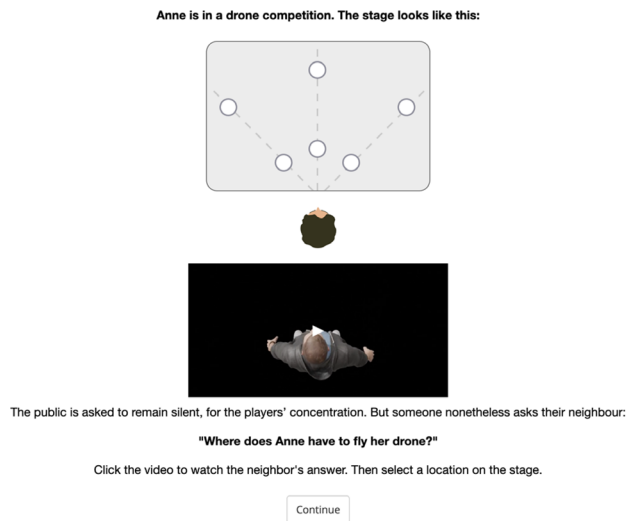
The viewer's task can be expected to involve different levels of difficulty: transposition requires mental rotation, which is certainly taxing; and duration is hard to interpret in absolute terms, especially without knowing the drone's speed. By contrast, direction without transposition can be expected to be easier.

(b) Results

Participants ($N = 98$) were presented with a sequence of trials displaying the setting described above. The gesture in each trial was composed of two meaningful components: Duration (short/long, coding for near/far **Distance**) and **Direction** (left/centre/right). In addition, there could be a **Rotation** of +90/−90/0° of the stage (with the drone pilot and its targets) relative to the gesturer. The sequence of trials was the factorial of all features, totalling $2 \times 3 \times 3 = 18$ trials. In a first block of trials, each participant was presented with all of these 18 trials in a randomized order. In a second block, all of these trials were presented again, in the same order as in the first block, anticipating a slower learning phase in participants for duration and transposition.

After watching each gesture video, participants had to select one of the six targets. We calculated average participant accuracy on the two gesture meanings: **Direction** and **Distance**. To test for transposition, we calculated

(A) No transposition needed



(B) Transposition needed

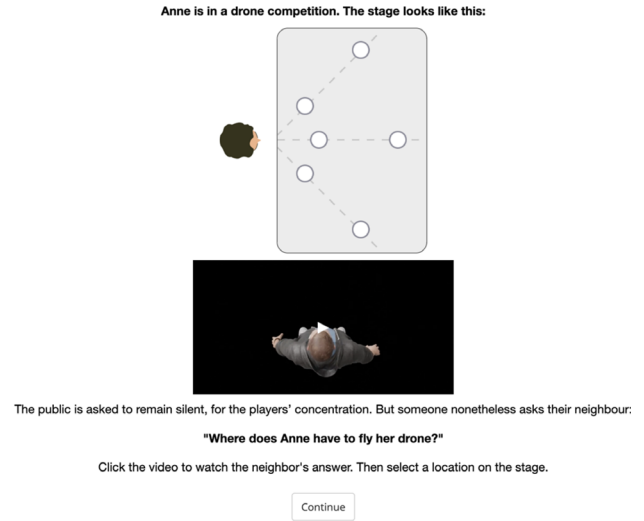
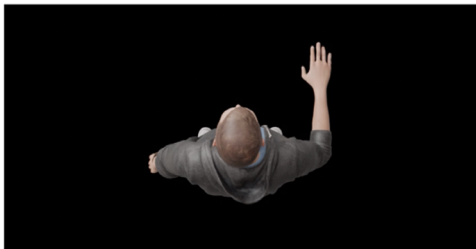


Fig. 17. Screenshots of the drone experiment. For a video with different trials demonstrating the expected answers, see: <https://youtu.be/I1HYEacCpc8>

(A) forward movement



(B) forward–rightward movement



Fig. 18. Two examples of manual gesture direction made by the avatar in our drone experiment.

accuracy for correct **Direction** answers separately; once for the two **Rotation** conditions: 90 and -90° degrees (transposition) and once for the 0° condition (no transposition). **Distance** accuracy was calculated over all **Rotation** angles.

We calculated significance ($P < 0.01$) compared to a chance baseline to check if participants significantly succeeded at detection of the relevant meanings in gesture. Chance was obtained by bootstrap: calculating target metrics on shuffled versions of the participants' actual responses.

The experiment setup and analysis were preregistered at <https://osf.io/z5ca4>, where all code also can be found.

Mean accuracy for **Direction** without transposition was 76.2% (compared to a 1/3 chance baseline); and 62.67% for **Direction** with transposition (compared to chance 1/3). Mean accuracy for **Distance** also passed the significance threshold compared to the chance baseline (52.6% compared to 50%), but it did so by a smaller margin. This

is in part due to participants ignoring this dimension altogether (e.g. eight participants responded 'long' for 36 out of 36 items; an additional six participants responded 'long' 35/36 times). We hypothesize that this could be related to the duration of the gesture, which is potentially hard to detect, or at least hard to interpret without an explicit point of comparison, something we also found in our ASL data, where our consultants were instructed to interpret sentences contrastively within a paradigm (note also that the modulation of classifier duration was arguably less natural than that of classifier direction).

(3) Taking stock

After observing that key properties of the waggle dance can be found in sign language classifiers, we showed that similar properties can also be found in some iconic gestures. While

our detailed sign language data were obtained from just two consultants (and co-authors), our gestural data were less detailed but more controlled, both in terms of stimuli (as the gesture was produced by an avatar) and data collection (experimental). The results fully dovetail with those of ASL classifiers: in our target examples, direction, duration and transposition are strongly reminiscent of the waggle dance. We did not test repetition because it seems to be a more general property of spoken and sign language expressions alike.

We conclude that the waggle dance is an iconic system that has a close relative in an unquestionable subpart of human language, namely sign language classifiers, and in iconic gestures, which are increasingly considered as essential components of language in linguistic research. These similarities should not obscure important differences, in particular the fact that (i) sign language classifiers (and iconic gestures) can describe many more things than just direction and duration, (ii) viewpoint shift is more flexible and context dependent than bee dance transposition, and (iii) classifier and gesture duration is interpreted in comparative (and context-dependent) terms, whereas bee dance duration is directly mapped to food distance.

VI. ANCESTRAL ICONICITY: PRIMITIVE WAGGLE DANCES

The waggle dance and sign language classifiers can thus be seen as different instantiations of an abstract iconic system. Their similarities are certainly not due to common descent. First, this is implausible because the most recent ancestor of humans and bees lived approximately 686 million years ago (e.g. Kumar *et al.*, 2022). Second, the waggle dance is a relatively recent innovation, dated to approximately 20 million years ago (FAnson Price & Grüter, 2015), and it is only found in one subfamily among bee species. Much older bee ancestors probably did not have the waggle dance, and there is no argument for the existence of an iconic system in them. For instance, the most recent ancestor of the large group of bees with a pollen basket (corbiculates, which include dancing bees) lived approximately 80 million years ago (Cardinal & Danforth, 2011) and certainly did not have a waggle dance.

The human incarnation of iconic signs and gestures is currently very difficult to date (see also A10 in Appendix S1). By contrast, the waggle dance can be reconstructed over millions of years, with exciting new questions about the nature of the ancestral (original) waggle dance.

(1) What was the ancestral waggle dance?

FAnson Price & Grüter (2015, p. 5) argue that the waggle dance is at least 20 million years old: ‘Extant honey bees diverged in the early Miocene (*ca.* 20 million years ago) (Engel, 2006; Cardinal & Danforth, 2011; Cardinal, Straka &

Danforth, 2010). Because all extant species use the “dance language”, we can be confident that their common ancestor also used a dance-based communication system (Oldroyd & Wongsiri, 2006; Raffiudin & Crozier, 2007). This provides a lower bound of *ca.* 20 million years before present for the evolution of the “dance language”. We also note that all bee species with a vertical dance exhibit the same transposition mechanism, despite the fact that other transposition mechanisms could be imagined and are observed in other insects (see also A11 in Appendix S1). This strengthens the case that vertical dancing with transposition emerged only once in the phylogeny.

But an important question remains open: which type of dance came first: the horizontal dance, without transposition, or the vertical dance, with transposition (here we follow the framing of Schlenker *et al.*, 2025b)? Several researchers, including Lindauer (1956), von Frisch (1967, e.g. p. 304) and Menzel (2019), suggested that the horizontal dance, which points directly towards the food source, was more primitive than the vertical dance, which involves transposition. There are two potential reasons for this idea. One is cognitive, as direct indication of direction is simpler and thus ‘more primitive’ than indication with transposition (e.g. von Frisch, 1967, p. 304). A second reason is concerned with the asymmetry mentioned above: several bee species that dance vertically (*Apis dorsata*, *Apis cerana*, *Apis mellifera*) can switch to a (directly pointing) horizontal dance, but *Apis florea*, which has a horizontal dance, does not adopt transposition when forced to dance vertically. This suggests that vertically dancing bees preserved an ability that was ancestral, namely horizontal dancing without transposition (e.g. Dyer, 1987). However, extant bee phylogenies in fact leave the question open, as we will see below.

(2) Comparing phylogenies

We sought to investigate the question of whether the ancestral dance was vertical or horizontal more systematically by comparing the different available phylogenies, as summarized in Fig. 19.

Raffiudin & Crozier (2007) (Fig. 19A) wrote: ‘there has been disagreement about whether the horizontal (Lindauer, 1961) or the vertical (Koeniger, 1976) dance form was the ancestral characteristic’ (p. 544). But their own results ‘give strong support to the ancestral honey bee nesting in the open’ (probability 98%), and ‘more likely than not’ having a silent waggle dance (probability 54%), a *vertical directional dance* (probability 67%) and a single comb (probability 69%) (p. 549).

A more recent phylogeny from Hedtke, Patiny & Danforth (2013) crucially positions *Apis dorsata* differently in the tree (Fig. 19B). There are eight species for which Raffiudin & Crozier (2007) provide information about their dance, of which seven are present in this phylogeny. We obtained a 99.7% probability that the common ancestor of these seven species danced vertically (see also A12 in Appendix S1).

Finally, we consider the most recent phylogeny from Almeida *et al.* (2023) (Fig. 19C). It contains four of the eight

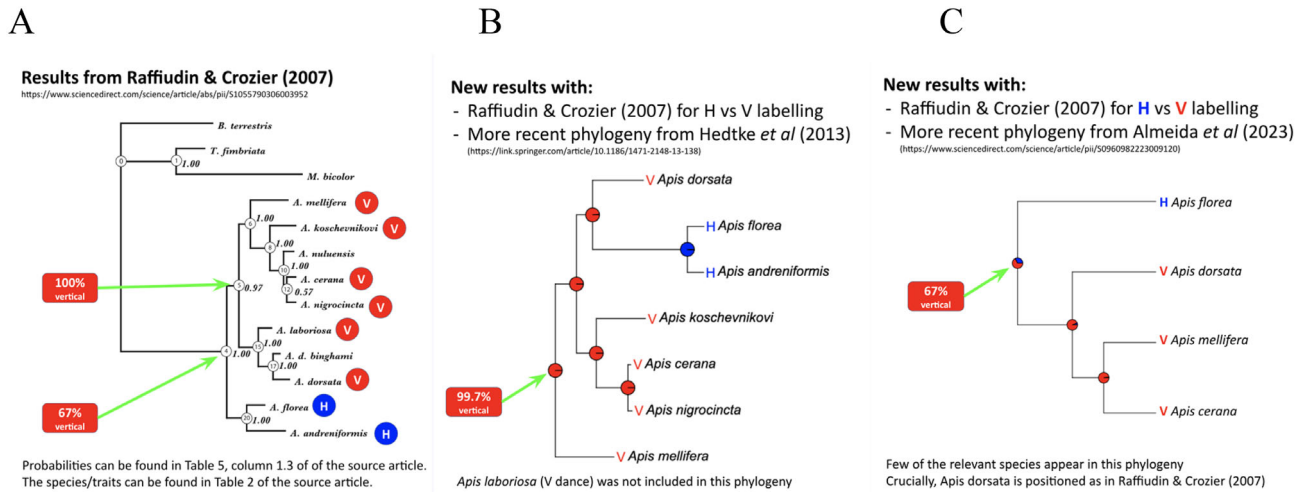


Fig. 19. Different phylogenies and the ancestral nature of the vertical dance. H = horizontal dance only; V = vertical dance.

species with dance information from Raffiudin & Crozier (2007), and crucially positions *Apis dorsata* in the same position as in Raffiudin & Crozier (2007). Accordingly, we obtained a 67% probability that the most recent common ancestor danced vertically.

In sum, there is a significant chance that the ancestral species danced vertically 20 million years ago. Depending on the position of *Apis dorsata* in the history of the species, support increases from 67% to 99%. Collecting data on the dance of more species could help refine the conclusion. However, the near-consensus in the literature that the original dance was horizontal might have to be revisited.

(3) How the vertical dance might have emerged first

If the vertical dance was ancestral, it remains to ask how it could have emerged. This is non-trivial because the vertical dance had to involve transposition, which is intuitively more complex to interpret than a dance without transposition.

A remarkable suggestion was made by several researchers, in particular von Frisch (1967, e.g. pp. 327–328), Lindauer (1971, p. 85), and Menzel (2019): a dance behaviour may exist in species without the corresponding signal. In Menzel's words (Menzel, 2019, p. 2), 'the most basic component is thought to be food-induced arousal, seen, for example, in the circling "dances" of the fly *Phormia regina* (...). Hungry flies run around a droplet of sugar water and continue performing such "dances" even when the sugar droplet is removed.' Crucially, 'when the surface is tilted from horizontal to vertical, they transfer the elongated runs they do, relative to light on the horizontal surface, to the upward direction on the vertical surface' (p. 2). von Frisch (1967) cited related transposition mechanisms in ants (*Myrmica ruginodis*, *Lasius niger*), ladybirds (*Coccinella septempunctata*), and dung beetles (*Geotrupes silvaticus*) (p. 326). von Frisch further noted that there is, more generally, a 'biologically meaningful' connection between orientation to light and to gravity:

bumblebees flying out into the open from their subterranean nest seek the light, but when displaced on a vertical surface (on their way into the open), they seek to go upwards, into the open (von Frisch, 1967, p. 327).

von Frisch (1967, p. 328) concluded that 'the phylogenetic step from the direct indication of direction to its transposition was facilitated by the fact that this capability is a primary possession of many insects'. But since this capability seems likely to have been present in the common ancestor of all dancing bees, it could also explain why transposition was available 'from the start', so to speak.

Still, if the vertical dance emerged first, a puzzle must be addressed. Why can vertically dancing bees have an ability to dance horizontally, without transposition? By contrast, why did horizontally dancing bees not preserve the ancestral ability to dance vertically, without transposition?

An alternative scenario might reconcile these conflicting arguments. The original dance could be horizontal but more ancient, having emerged some time *before* the most recent common ancestor of modern bees. Vertical dancing with transposition might have emerged after horizontal dancing, but still before the most recent common ancestor. Vertical dancing then survived into most modern species, but was lost on the branch leading to the last common ancestor of *Apis florea* and *Apis andreniformis*.

The question is thus open and both hypotheses (horizontal *versus* vertical ancestral dance) should be investigated in future research. A summary of the arguments for and against these two main hypotheses (horizontal first *versus* vertical first) appears in Table 2.

VII. FUTURE DIRECTIONS

Our comparative discussion of the waggle dance and of iconic constructions of sign language should be seen as a

Table 2. Arguments regarding the nature of the ancestral waggle dance.

Arguments	Hypothesis they support	Reasoning
Cognitive complexity	Horizontal first	The horizontal dance is cognitively simpler than the vertical dance because the latter involves transposition.
'Bilingualism' (species that have two modes of dancing)	Horizontal first	Vertically dancing bees (<i>A. dorsata</i> , <i>A. cerana</i> , <i>A. mellifera</i>) can switch to a horizontal dance without transposition. The horizontally dancing bee <i>A. florea</i> never uses transposition. This can be explained if vertical dancing is a later innovation and horizontal dancing was preserved after the innovation.
Phylogenies	Vertical first	Extant phylogenies give a probability between 67% and 99% that the most recent common ancestor danced vertically.

contribution to a more general typology of iconic systems in nature, with a precise delineation of the operations (such as Duration, Direction, Transposition and Repetition) that are or are not found in different species, including humans. Iconicity is not a monolith (Greenberg, 2023), and a precise formal approach could give rise to an articulated typology. The extraordinary strength of bee research was to show with great clarity that, along three dimensions, gradient modifications of form lead to gradient modifications of meaning. Evidencing similar gradient effects in further species would be an important contribution to a general typology of iconic operations in nature.

In the case of bees, the evolutionary history of the waggle dance should be revisited. On the standard view, the horizontal dance was ancestral, in the sense of being present in the most recent common ancestor of extant dancing bees, and the vertical dance was a later development. In some phylogenies (see Fig. 19A,C), transposition might have evolved only once among bees, in the common ancestor of vertically dancing bees. On an alternative view, the vertical dance was ancestral, and the mechanism of transposition might have existed at that point or much earlier, as suggested by the existence of transposing mechanisms in insects without a dance. What is surprising is that ancestral vertically dancing bees could likely dance horizontally as well; this might suggest that a horizontal dance existed at that point or earlier (potentially,

before the most recent common ancestor of all extant dancing bees). This open question should be investigated in greater detail. More generally, future research should seek to retrace the evolutionary history of the key properties of the waggle dance (not just Transposition, but also Duration, Direction and Repetition).

VIII. CONCLUSIONS

- (1) The view that the waggle dance lacks interesting properties of human language is erroneous. Although human language has a discrete, symbolic module that is entirely different from the waggle dance, it also contains rich iconic constructions, notably sign language classifiers, which have important properties in common with the waggle dance.
- (2) Specifically, in sign language classifiers and in iconic gestures, duration and direction are interpreted gradiently, and viewpoint shift (a more general form of transposition) can be effected. In addition, throughout human language and probably animal communication, repetition can be used to convey greater importance or urgency. Four key properties of the waggle dance are thus exemplified in human language.
- (3) von Frisch's use of the term 'dance language of bees' makes sense: while the waggle dance differs from the discrete core of human language, it bears a striking similarity to constructions found in its iconic module.
- (4) The evolutionary history of the waggle dance shows that a sophisticated iconic system existed in nature at least 20 million years ago.
- (5) While the accepted view is that the dance without viewpoint shift was ancestral, a more detailed analysis of extant phylogenies suggests that the vertical dance might well have been ancestral.
- (6) The existence of pre-adaptations might have guaranteed that transposition (viewpoint shift) was available from the start, thus explaining why the apparently more complex dance might have emerged first.

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We dedicate this piece to the memory of Anita Janda, whose 1978 dissertation on *The Linguistic Analysis of the Honey Bee's Dance Language* anticipated by 40 years what is now called 'animal linguistics'. Anita Janda died in 2006; a eulogy can be found here: <https://ashsherlockian.org/anita-janda-ash/>. This research received funding (to P. S., L. R. and A. S.) from the European Research Council (ERC) under the European Union's Horizon 2020 research and innovation programme (grant agreement No 788077, Orisem, PI: to P. S.). The research of P. S., L. R. and E. C. was conducted at DEC, Ecole Normale Supérieure – PSL Research University. DEC is supported by grant FrontCog ANR-17-EURE-0017. We are grateful to two anonymous reviewers for very perceptive

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X. REFERENCES

References identified with an asterisk (*) are cited only within the online Supporting Information.

- ALMEIDA, E., BOSSERT, S., DANFORTH, B., PORTO, D., FREITAS, F., DAVIS, C., MURRAY, E., BLAIMER, B., SPASOJEVIC, T., STRÖHER, P., ORR, M., PACKER, L., BRADY, S., KUHLMANN, M., BRANSTETTER, M. & PIE, M. (2023). The evolutionary history of bees in time and space. *Current Biology* **33**, 1–14.
- ANDERSON, S. R. (2004). *Dr. Dolittle's Delusion In Animals and the Uniqueness of Human Language*. Yale University Press, New Haven, USA.
- BENVENISTE, E. (1953). Animal communication and human language: the language of the bees. *Diogenes* **1**(1), 1–7.
- BIESMEIJER, J. C. & SEELEY, T. D. (2005). The use of waggle dance information by honey bees throughout their foraging careers. *Behavioral Ecology and Sociobiology* **59**(1), 133–142.
- *BIRUKOW, G. (1954). Photo-Geometotaxis bei *Geotrupes silvaticus* Panz. Und ihre zentralnervöse Koordination. *Zeitschrift für Vergleichende Physiologie* **36**, 176–211.
- BOOK, D. L. & FREEBERG, T. M. (2015). Titmouse calling and foraging are affected by head and body orientation of cat predator models and possible experience with real cats. *Animal Cognition* **18**(5), 1155–1164.
- *BYRNE, R. W., CARTMILL, E., GENTY, E., GRAHAM, K. E., HOBAITER, C. & TANNER, J. (2017). Great ape gestures: intentional communication with a rich set of innate signals. *Animal Cognition* **20**(4), 755–769.
- CARDINAL, S. & DANFORTH, B. N. (2011). The antiquity and evolutionary history of social behavior in bees. *PLoS One* **6**(6), e21086.
- CARDINAL, S., STRAKA, J. & DANFORTH, B. N. (2010). Comprehensive phylogeny of apid bees reveals the evolutionary origins and antiquity of cleptoparasitism. *Proceedings of the National Academy of Sciences* **107**(37), 16207–16211.
- CHOMSKY, N. (1975). Knowledge of language. In *Language, Mind and Knowledge* (ed. K. GUNDERSON), pp. 299–320. University of Minnesota Press, Minneapolis.
- CORBALLIS, M. C. (1993). *The Lopsided Ape: Evolution of the Generative Mind*. Oxford University Press, New York, USA.
- COURTER, J. R. & RITCHISON, G. (2010). Alarm calls of tufted titmouse convey information about predator size and threat. *Behavioral Ecology* **21**(5), 936–942.
- DAHL, J. A. & RITCHISON, G. (2018). Responses of blue jays (*Cyanocitta cristata*) to raptors that differ in predatory threat. *Avian Biology Research* **11**(3), 159–166.
- DAVIDSON, K. (2015). Quotation, demonstration, and iconicity. *Linguistics & Philosophy* **38**(6), 477–520.
- DUTOUR, M., SUZUKI, T. N. & WHEATCROFT, D. (2020). Great tit responses to the calls of an unfamiliar species suggest conserved perception of call ordering. *Behavioral Ecology and Sociobiology* **74**(3), 37.
- DYER, F. C. (1987). New perspectives on the dance orientation of the Asian honeybees. In *Neurobiology and Behavior of Honeybees* (eds R. MENZEL and A. R. MERCER), pp. 54–65. Springer-Verlag, Berlin-Heidelberg-New York.
- *DYER, F. C. (2019). Dance language. In *Encyclopedia of Animal Behavior* (ed. J. C. CHOE), pp. 682–690. Academic Press.
- EARL, B. (2023). Humans, fish, spiders and bees inherited working memory and attention from their last common ancestor. *Frontiers in Psychology* **13**, 937712.
- EMMOREY, K. (2014). Iconicity as structure mapping. *Philosophical Transactions of the Royal Society of London B* **369**, 20130301.
- EMMOREY, K. & HERZIG, M. (2003). Categorical versus gradient properties of classifier constructions in ASL. In *Perspectives on Classifier Constructions in Sign Languages*, pp. 231–256. Psychology Press.
- ENGEL, M. S. (2006). A giant honey bee from the middle Miocene of Japan (hymenoptera: Apidae). *American Museum Novitates* **3504**, 1–12.
- ESCH, H. E. (2012). Foraging honey bees: how foragers determine and transmit information about feeding site locations. In *Honeybee Neurobiology and Behavior* (eds C. GALIZIA, D. EISENHARDT and M. GIURFA), pp. 53–64. Springer, Dordrecht.
- ESCH, H. E., ZHANG, S., SRINIVASAN, M. V. & TAUTZ, J. (2001). Honeybee dances communicate distances measured by optic flow. *Nature* **411**(6837), 581–583.
- GARDNER, K. E., SEELEY, T. D. & CALDERONE, N. W. (2008). Do honeybees have two discrete dances to advertise food sources? *Animal Behaviour* **75**(4), 1291–1300.
- GOLDIN-MEADOW, S. & BRENTARI, D. (2017). Gesture, sign and language: the coming of age of sign language and gesture studies. *Behavioral and Brain Sciences* **40**, e46.
- *GOULD, J. L. (1975). Honey bee communication: the dance language controversy. Thesis, Rockefeller University.
- GREENBERG, G. (2023). The iconic-symbolic spectrum. *Philosophical Review* **132**(4), 579–627.

- GRÜTER, C. & FARINA, W. M. (2009). The honeybee waggle dance: can we follow the steps? *Trends in Ecology & Evolution* **24**(5), 242–247.
- HEDTKE, S. M., PATINY, S. & DANFORTH, B. N. (2013). The bee tree of life: a supermatrix approach to apoid phylogeny and biogeography. *BMC Evolutionary Biology* **13**(1), 138.
- I'ANSON PRICE, R. & GRÜTER, C. (2015). Why, when and where did honey bee dance communication evolve? *Frontiers in Ecology and Evolution* **3**, 125.
- JANDA, A. (1978). The linguistic analysis of the honey bee's dance language. Doctoral dissertation, CUNY.
- KOENIGER, N. (1976). Neue Aspekte der Phylogenie innerhalb der Gattung *Apis*. *Apidologie* **7**, 357–366.
- KRYŠTOFKOVÁ, M., HAAS, M. & EXNEROVÁ, A. (2011). Nest defense in blackbirds *Turdus merula*: effect of predator distance and parental sex. *Acta Ornithologica* **46**(1), 53–61.
- KUMAR, S., SULESKI, M., CRAIG, J. M., KASPROWICZ, A. E., SANDERFORD, M., LI, M., STECHER, G. & HEDGES, S. B. (2022). TimeTree 5: an expanded resource for species divergence times. *Molecular Biology and Evolution* **39**(8), msac174.
- LEAVESLEY, A. J. & MAGRATH, R. D. (2005). Communicating about danger: urgency alarm calling in a bird. *Animal Behaviour* **70**(2), 365–373.
- LEMASOON, A., OUATTARA, K., BOUCHET, H. & ZUBERBÜHLER, K. (2010). Speed of call delivery is related to context and caller identity in Campbell's monkey males. *Naturwissenschaften* **97**(11), 1023–1027.
- LIDDELL, S. K. (2003a). *Grammar, Gesture, and Meaning in American Sign Language*. Cambridge University Press, Cambridge.
- LIDDELL, S. K. (2003b). Sources of meaning in ASL classifier predicates. In *Perspectives on Classifiers in Sign Languages* (ed. K. EMMOREY), p. 199220. Lawrence Erlbaum, Mahwah, NJ.
- LINDAUER, M. (1956). Über die Verständigung bei indischen Bienen. *Zeitschrift für Vergleichende Physiologie* **38**(6), 521–557.
- LINDAUER, M. (1961). *Communication among Social Bees*. Harvard University Press, Cambridge.
- LINDAUER, M. (1971). *Communication among Social Bees*. Harvard University Press, Cambridge.
- LUDDEN, D. (2015). *The Psychology of Language: An Integrated Approach*. SAGE Publications, London, UK.
- MACSWEENEY, M., CAPEK, C. M., CAMPBELL, R. & WOLL, B. (2008). The signing brain: the neurobiology of sign language. *Trends in Cognitive Sciences* **12**(11), 432–440.
- MALAN, G., SEORAJ-PILLAI, N. & DU PLESSIS, M. A. (2009). Alarm calls of bronze mannikins communicate predator size to familiar conspecifics. *Ostrich* **80**(3), 177–184.
- MCRAE, T. R. (2020). A review of squirrel alarm-calling behavior: what we know and what we do not know about how predator attributes affect alarm calls. *Animal Behavior and Cognition* **7**(2), 168–191.
- MENZEL, R. (2019). The waggle dance as an intended flight: a cognitive perspective. *Insects* **10**(12), 424.
- MICHELESEN, A. (2012). How do honey bees obtain information about direction by following dances? In *Honeybee Neurobiology and Behavior* (eds C. GALIZIA, D. EISENHARDT and M. GIURFA). Springer, Dordrecht.
- MURPHY, D., LEA, S. E. & ZUBERBÜHLER, K. (2013). Male blue monkey alarm calls encode predator type and distance. *Animal Behaviour* **85**(1), 119–125.
- OLDROYD, B. P. & WONGSIRI, S. (2006). *Asian Honey Bees: Biology, Conservation, and Human Interactions*. Harvard University Press, Cambridge, MA.
- *PATEL-GROSZ, P. (2023). The search for universal primitive gestural meanings. *Proceedings of Sinn und Bedeutung* **27**, 500–518.
- PYERS, J. E., PERNISS, P. & EMMOREY, K. (2015). Viewpoint in the visual-spatial modality: the coordination of spatial perspective. *Spatial Cognition & Computation* **15**(3), 143–169.
- *QUER, J. (2013). Attitude ascriptions in sign languages and role shift. In *Proceedings of the 13th Meeting of the Texas Linguistics Society*, pp. 12–28. University of Texas, Texas Linguistics Forum, Austin.
- RAFFIUDIN, R. & CROZIER, R. H. (2007). Phylogenetic analysis of honey bee behavioral evolution. *Molecular Phylogenetics and Evolution* **43**(2), 543–552.
- RILEY, J. R., GREGGERS, U., SMITH, A. D., REYNOLDS, D. R. & MENZEL, R. (2005). The flight paths of honeybees recruited by the waggle dance. *Nature* **435**(7039), 205–207.
- SANDLER, W. & LILLO-MARTIN, D. (2006). *Sign Language and Linguistic Universals*. Cambridge University Press, New York.
- SCHEMBRI, A., JONES, C. & BURNHAM, D. (2005). Comparing action gestures and classifier verbs of motion: evidence from Australian sign language, Taiwan sign language, and nonsigners' gestures without speech. *Journal of Deaf Studies and Deaf Education* **10**(3), 272–290.
- SCHLENKER, P., BONNET, M., LAMBERTON, J., LAMBERTON, J., CHEMLA, E., SANTORO, M. & GERACI, C. (2024). Iconic syntax: sign language classifier predicates and gesture sequences. *Linguistics & Philosophy* **47**, 77–147.
- SCHLENKER, P., CHEMLA, E., SCHEL, A., FULLER, J., GAUTIER, J. P., KUHN, J., VESELINOVIC, D., ARNOLD, K., ČÁŠAR, C., KEENAN, S., LEMASSON, A., OUATTARA, K., RYDER, R. & ZUBERBÜHLER, K. (2016). Formal monkey linguistics. *Theoretical Linguistics* **42**(1–2), 1–90.

- *SCHLENKER, P. & LAMBERTON, J. (2019). Iconic plurality. *Linguistics & Philosophy* **42**, 45–108.
- *SCHLENKER, P. & LAMBERTON, J. (2022). Meaningful blurs: the sources of repetition-based plurals in ASL. *Linguistics & Philosophy* **45**, 201–264.
- SCHLENKER, P. & LAMBERTON, J. (2024). Iconological semantics. *Linguistics and Philosophy* **47**(5), 779–838.
- *SCHLENKER, P., LAMBERTON, J. & LAMBERTON, J. (2025a). Context Shift and Viewpoint Shift: Super Monsters Revisited. Manuscript, Institut Jean-Nicod.
- SCHLENKER, P., LAMBERTON, J. & SANTORO, M. (2013). Iconic variables. *Linguistics & Philosophy* **36**, 91–149.
- SCHLENKER, P., PAWLOWITSCH, C., ARNAL, L., CHATAIN, K., RAVAUX, L., RYDER, R., SALIS, A., STEINERT-THRELKELD, S., WANG, L. & CHEMLA, E. (2025b). Ancestral meanings: a prelude to evolutionary animal linguistics. *Linguistics & Philosophy* **48**(5), 823–878.
- SCHÜRCH, R., ZWIRNER, K., YAMBRICK, B. J., PIRAULT, T., WILSON, J. M. & COUVILLON, M. J. (2019). Dismantling babel: creation of a universal calibration for honey bee waggle dance decoding. *Animal Behaviour* **150**, 139–145.
- SEELEY, T. D., MIKHEYEV, A. S. & PAGANO, G. J. (2000). Dancing bees tune both duration and rate of waggle-run production in relation to nectar-source profitability. *Journal of Comparative Physiology A* **186**(9), 813–819.
- TEMPLETON, C. N., GREENE, E. & DAVIS, K. (2005). Allometry of alarm calls: black-capped chickadees encode information about predator size. *Science* **308**(5730), 1934–1937.
- TUTTLE, R. H. (2014). *Apes and Human Evolution*. Harvard University Press, Cambridge, MA and London, England.
- VALLI, C. & LUCAS, C. (2000). *Linguistics of American Sign Language: An Introduction*. Gallaudet University Press, Washington, DC.
- VON FRISCH, K. (1954). Symbolik im Reich der Tiere. Münchner Universitätsreden, N. F., H. 7 (Munich, 1954).
- VON FRISCH, K. (1967). *The Dance Language and Orientation of Bees*. Harvard University Press, Boston, MA. Translated by Leigh E. Chadwick. With a New Foreword by Thomas D Seeley. Second printing, 1993.
- ZUCCHI, S. (2011). Event descriptions and classifier predicates in sign languages. Presentation at FEAST (Formal and Experimental Advances in Sign language Theory) in Venice, June 21, 2011.
- ZUCCHI, S. (2017). Event categorization in sign languages. In *Handbook of Categorization in Cognitive Science*, Second Edition (eds H. COHEN and C. LEFEBVRE), pp. 377–396. Elsevier, Amsterdam.
- ZUCCHI, S. (2018). Sign language iconicity and gradient effects. *Theoretical Linguistics* **44**(3–4), 283–294.
- ZWITSERLOOD, I. (2012). Classifiers. In *Sign Language: An International Handbook* (eds R. PFAU, M. STEINBACH and B. WOLL), pp. 158–186. De Gruyter Mouton, Berlin, Boston.

XI. SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section at the end of the article.

Appendix S1. List of information additional to the main text referred to in the main text by numbered points.

Appendix S2. Sign language data.

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