

Shared semantics: Exploring the interface between human and chimpanzee gestural communication

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Abstract

Striking similarities across ape gestural repertoires suggest shared phylogenetic origins that likely provided a foundation for the emergence of language. We pilot a novel approach for exploring possible semantic universals across human and nonhuman ape species. In a forced-choice task, $n = 300$ participants watched ten chimpanzee gesture forms performed by a human and chose from responses that paralleled inferred meanings for chimpanzee gestures. Participants agreed on a single meaning for nine gesture forms; in six of these the agreed form-meaning pair response(s) matched those established for chimpanzees. Such shared understanding suggests apes' (including humans') gesturing shares deep evolutionary origins.

Keywords

gesture, primates, communication, manual modality, form-meaning mappings, pragmatics

1. INTRODUCTION

There remains substantial debate over when and how language emerged in modern human communication (e.g., Fitch, 2010). Recent developments in primatology have led to an increase in data on non-human great ape (hereafter “ape”) gesture forms and meanings (see e.g., Tomasello et al., 1985, 1994; Pika, Liebal & Tomasello, 2005; Pika et al., 2005; Liebal, Pika & Tomasello, 2006; Graham et al., 2018; Hobaiter & Byrne, 2011, 2014, 2017; Bard et al., 2014; Byrne et al., 2017; Byrne & Cochet, 2017; Fröhlich et al., 2017). Simultaneously, there is a large and growing body of literature on gesture in humans (see e.g., Kendon, 1980, 1995, 2004; McNeill, 1992, 2012; Kita, 2009; Streeck, 2009; Calbris, 2011; Abner, Cooperrider & Goldin-Meadow, 2015; Müller, 2004, 2017). This rapid expansion of interest has brought with it challenges in aligning the work across human and non-human ape gesture, with a diversity of approaches taken to how gesture is operationalised within humans and other apes (Rodrigues et al., 2021; Abner et al., 2015; Bourjade et al., 2020; Kendon, 2004; Cartmill & Hobaiter, 2019).

An important question that has gained prominence in gesture research concerns the existence of gestural *universals*, for example considering the presence of universal gesture forms (and even gestural form-meaning pairings) across cultures within the human species

(see for, e.g., palm-up gestures: Cooperrider, Abner & Goldin-Meadow, 2018; Cooperrider, 2019); and across ape species (Byrne et al., 2017). Recent studies comparing human and ape gesture found striking similarities—pre-linguistic 1-year to 2-year-old human infants naturally used 46 “ape-typical” gesture forms (Kersken et al., 2019); and language proficient human adults correctly interpreted the meanings of commonly occurring chimpanzee and bonobo gesture forms as proposed in primatology research (Graham & Hobaiter, 2023). These species overlaps suggest that a similar gestural repertoire was plausibly present in the last common ancestor of all humans, bonobos and chimpanzees, ~7.6 million years ago (Pozzi et al., 2014).

Relatedly, recent research in semantics proposed the existence of semantic universals in the shape of abstract meaning *components* (or *atoms*), which are generalised fragments of meaning found across languages, that all humans have access to and that then form parts of more complex meanings (e.g., May, 1991; Partee, 1992; Goddard, Cliff & Wierzbicka, 1994, 2018; Wierzbicka, 1996, 2013; von Stechow & Matthews, 2008; Steinert-Threlkeld & Szymanik, 2020). In tandem, recent work comparing gesture use across great ape species, on the basis of which gesture meanings are inferred, has found that chimpanzees and bonobos (whose last common ancestor lived ~1 to 1.8 million years ago, Takemoto et al., 2017; Pozzi et al., 2014) overlap to an extent that is greater than expected by chance, supporting a shared origin of understanding gestural meanings (Graham et al., 2018).

Bringing these perspectives on gesture form and meaning perspectives together, we move beyond established similarities of gestural forms across primate species (Byrne et al., 2017; Kersken et al., 2019) and ask whether there are abstract gestural form-meaning pairings that are shared between humans and other great apes. To do so, we ask whether these “ape” gestures can also be performed as human gestures that communicate comparable meanings. From a big picture perspective, we are not looking for concrete semantic meanings of gestural forms here (such as a universal gesture for “Move away”); this has already been unsuccessfully attempted elsewhere (e.g., Cooperrider, 2019). Rather, we are exploring how some abstract meaning atoms may form an underlying structure to gesture production in apes, with our intended level of abstractness being exemplified by abstract notions such as the *encouragement* of some exchange (Figure 1a) or its *discouragement* (Figure 1b). Therefore,

for this study, we chose to use a broad definition of *gesture* as “a communicative body movement” (illustrated in Figure 1).

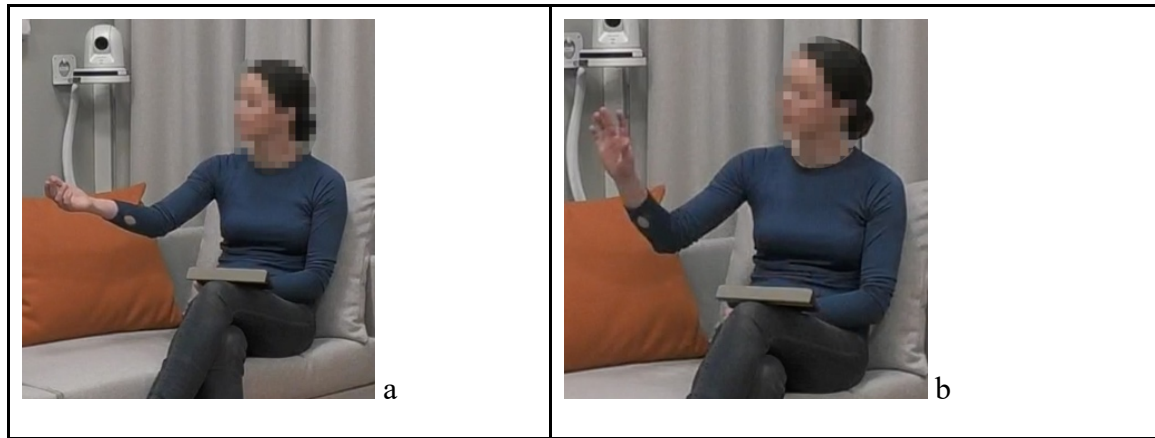


FIGURE 1. Examples of gesture forms at the end of their production phase. Panel (a) *Reach palm* (a palm-up open-hand gesture); panel (b) *Hand fling* (addressee-facing open-hand gesture).

Universal gestural form-meaning pairings, in the sense that they are shared by humans and other apes, if they exist, may be a result of shared biological inheritance—for example, African apes living in distinct environments share ~90% of their gestural repertoires (e.g., Byrne et al., 2017). From an evolutionary perspective, this extensive overlap within African apes naturally suggests an innate component; however, gestural commonalities may also result from shared physical/cognitive needs and capacities in early communicative exchanges (e.g., Plooij, 1984). For example, requests to “Move closer”, “Move away”, or “Give it to me” are likely to be common communicative acts resulting from shared needs across all apes and require similar cognitive capacities, such as the recognition of others as distinct agents and, in some cases, the ability to refer to external items of interest (Hobaiter, Leavens & Byrne, 2014). Similarly, humans and apes share similar body plans (e.g., joint/limb configuration and similar sensory perceptions) as well as having comparable interactions with their external world (e.g., the meaning “Move away” of a *Push* gesture, as shared by bonobos and chimpanzees, may be co-opted from the physical action of pushing something away).

An important distinction between biological research on non-human animals and linguistic research on human communication concerns their respective null hypotheses. In biological research, the typical null hypothesis for the origin of similar features between closely related species would be its shared emergence in a common ancestor; so for our study, the biological null hypothesis is that ape-typical gesture form-meaning pairings would be derived from a *phylogenetic* origin (= *phylogenetic gesture* hypothesis). By contrast, the typical linguistic null hypothesis assumes that communicative form-meaning pairings (such as the many used in language) are acquired/learned during an individual's lifetime; so the linguistic null hypothesis here is that ape-typical gesture form-meaning pairings are similarly acquired/learned by each species (= *acquired gesture* hypothesis). While any single hypothesis that falls too heavily to one side of this classic "nature versus nurture" debate almost certainly does not fully encapsulate the complex story behind the evolution of gesture form-meaning pairs in apes, much of the research in wild apes suggests some correspondences owing to a phylogenetic origin in, at least, form. For example, ontogenetic ritualization (a proposed process where fully functional actions become truncated into communicative signals through repeated interactions between conspecifics and their environment) may help explain some gestural form-meaning pairings between specific individuals (Plooij, 1984; Halina, Rossano & Tomasello, 2013), it does not predict the substantial overlap of gestural repertoires across individuals, communities, and species that has been found in wild apes (e.g., Hobaiter & Byrne, 2011; Byrne et al., 2017; Graham et al., 2018). Additionally, the finding that the chimpanzee gestural repertoire only employs 12.3% of their *possible maximum repertoire size* (Hobaiter & Byrne, 2017) exemplifies the level of diversity that could exist even within a species, but simply does not. Iconicity may also give rise to shared form-meaning pairings; however, the presence of iconicity in apes, as well as the extent to which the apes perceive it, remains debated (Tanner & Byrne, 1996; Pika & Mitani, 2006; Moore, 2014; Genty & Zuberbühler, 2015; Byrne et al., 2017; Tramacere & Moore, 2018).

We have now reached a point where the empirical findings within primatology and linguistics can inform one another. Here we pilot an inter-disciplinary method that applies and refines recently established experimental methodology (Graham & Hobaiter, 2023) for the exploration of ape gestures to modern language-using humans. Gestural studies in great apes have focused on the gestures' use as *imperative demands*, where the signaller requests

the recipient to make something happen in the external world (e.g., Pika, Liebal & Tomasello, 2005; Pika et al., 2005; Pika, 2008; Hobaiter & Byrne, 2014; Graham et al., 2018). These gestural requests require behavioural responses that are readily observable; based on such observations, researchers can infer the gestures' meaning (Cartmill & Byrne, 2007; Hobaiter & Byrne, 2014), but this approach potentially fails to capture a wider range of other (non-imperative) types of meanings. Nevertheless, furthering our understanding of the universal features of gesture in great apes begins with such gestures; in linguistic research, these imperative demands can be classified as *directives* (or directive speech acts), that is “attempts ... by the speaker to get the hearer to do something” (Searle, 1975, p. 355). We thus label them as *directive gestures*.

When viewing the current research from this combined (primatology-linguistics) perspective, we hypothesize that the communication of directive meanings via gestural forms in great ape species might still be contained in the gesturing of humans, providing a structure of “core-meanings” that are integrated into human communicative interactions due to their universal nature, and which are potentially further built upon in the generation of more complex meanings.

We investigate whether, when viewing a chimpanzee gesture with an established chimpanzee meaning, which was subsequently produced by a human, adult humans infer the same meaning(s) as attested in chimpanzees. To address this, we ask: Do adult humans agree on the same meaning(s) for a particular gesture form, and to what extent do they infer the same meaning inference(s) as chimpanzees?

2. METHODS

We created 10 brief videos of commonly used chimpanzee gestures for which we had established chimpanzee meanings (see Supplemental Materials for details on gesture form-meaning pairings and their selection) performed by a human adult, CH, who is an expert in chimpanzee gestures (hereafter, the signaller), directed at another human adult, PP-G (hereafter, the recipient). These videos were shown to adult human participants ($n=300$) in a forced choice task with four possible responses. All response options were based on meanings for which chimpanzees use their gestures. One (*Tight* gesture forms) or two (*Flexible* gesture

forms, see below) of these response options matched the most frequent meaning(s) in chimpanzees' use of each gesture. The remaining three (or two) response options were distractors, taken from meanings used for other gesture forms. Participants were prompted to select which of these four responses they thought the signaller wanted to communicate to the recipient by means of their performed gesture. Participants in the study were not informed in advance that they were viewing gestures from the chimpanzee repertoire or given any indication that this may be the case; instead, they were fully debriefed on this and other aspects after taking the study.

2.1 Selection of Gesture forms and meaning paraphrases

Our experiment applied the methodology of the *Great Ape Dictionary* experiment (see methods: <https://greatapedictionary.ac.uk/experiment> by Graham & Hobaiter, 2023), which employed a forced-choice paradigm, a frequently used method in psychological studies to access implicit understanding or knowledge. In the *Great Ape Dictionary* experiment, participants were presented with a video of an ape gesture and offered four responses to choose from. Here, we recreated chimpanzee gesture forms with established chimpanzee meanings in a human-human interaction.

Great apes have large repertoires of ~80 gesture forms (Byrne et al., 2017; Hobaiter & Byrne, 2011; Graham, Furuichi & Byrne, 2017). The 10 gesture forms (Table S1) that we used here were chosen on the grounds that: firstly, they could plausibly occur in a naturalistic interaction between two humans – ruling out non-manual gestures such as *Side Roulade* (description: “Body is rotated around the head-feet axis while lying on the ground with horizontal displacement along the ground” from Hobaiter & Byrne, 2011), or manual gestures such as *Big loud scratch* (description: “Loud exaggerated scratching movement on the signaller’s own body” from Hobaiter & Byrne, 2011). Secondly, their objective meanings would be plausible in an exchange between two adult humans in an informal setting – we did not include gestures where the chimpanzee meanings were improbable or inappropriate, including sexual behaviour, grooming, and carrying. The ape gesture forms used were established in studies that define gesture as “discrete, mechanically ineffective physical movements of the body observed during periods of intentional communication” (e.g., Hobaiter & Byrne, 2011). As a result, while contact gestures such as *Push* and *Grab Hold*

were included, they explicitly could not function as signals that achieved their goals through mechanical force.

In chimpanzees, Hobaiter and Byrne (2014) infer the signallers' intended meanings based on their *apparently satisfactory outcomes* (ASO). ASOs refer to reactions on the part of the recipient that makes the signaller stop gesturing; for example, if a signaller performs an *Arm Raise* gesture and stops performing the gesture when the receiver starts approaching the signaller, then we conclude that the gesture's meaning was "Move closer". This usage-based approach to the meanings of gestures uses the term *meaning* in a sense that descriptively captures the successful use of a gesture in a given instance and uses multiple successful instances to construct a distribution of meaning(s) for that gesture form, which is how we use the term throughout this paper. This does not preclude the existence of more abstract underlying gesture meanings, in the sense that the meanings "Move away" and "Stop that" may be contextual realizations of a more abstract negative meaning that constitutes the gesture's *lexical entry* (such as a non-specified "Stop" meaning, which may be contextually enriched to "Stop being so close" or "Stop your current activity", as proposed in Patel-Grosz 2023). Important updates on the chimpanzee gestural repertoire from Hobaiter and Byrne (2014) that inform Table S1 include Byrne et al. (2017), in which the gesture *Grab* was split into *Grab* and *Grab Hold*, and the gesture *Reach* was split into *Reach palm* and *Reach wrist*.

Note that there is no one-to-one correspondence between gesture forms and their meanings, as illustrated above with the construction of meaning distributions across multiple successful gesture instances; gestures may have more than one meaning, and some meanings are expressed by more than one gesture. For instance, the gesture forms *Arm raise* and *Beckon* can both communicate "Move closer" in chimpanzees, while *Hand fling* and *Hit object* can both communicate "Move away". The use of a single gesture form to communicate multiple meanings can complicate analyses, particularly where some meanings may be genuine but rarely expressed, while others may represent noise or misunderstanding by observers. Cartmill and Byrne (2010), distinguished *tight*, *loose*, and *ambiguous* gestures based on the specificity of outcome matching (see also Hobaiter & Byrne, 2014); here we follow a similar approach and considered two broad categories of gestural flexibility: *Tight gestures* were considered to have a single meaning where there was a single outcome associated with successful use in over 60% of cases; and *Flexible gestures* were considered to have two

meanings where no single outcome was associated with use in more than 60% of cases and two or more outcomes were regularly, and successfully, achieved by this gesture.

Four of our ten gestures were Tight and six were Flexible. We included two meanings of Flexible gestures to represent their multiple correct meanings. As our data do not represent a specific instance of ape usage in which one meaning was intended (compare with Graham & Hobaiter, 2023), both meanings were considered equally correct in the video interactions. In our statistical analysis, we thus consider both meanings for Flexible gestures to reflect an “expected” response. In practice, this meant that for Tight gestures (where one in four options was correct) chance level was at 25%, whereas for Flexible gestures (where two of four options were correct) chance level was at 50%. One risk of including two “correct” responses for Flexible gesture forms is that the answers of participants who intuit a correct response may be split across the two correct responses; however, we considered this to be the methodologically conservative approach and account for it in our analyses. A further disadvantage of including both correct responses is that it may make the results more difficult to interpret; however, this way we avoid *a priori* decisions, eliminating experimenter influence on which of the correct responses should be considered “more correct” than the other.

In previous literature, ASO-based great ape gesture meanings were described as statements such as “Acquire object”, which are not necessarily intuitive for gestures performed by a human, so we created more natural “translations” (e.g., “Give it to me” instead of “Acquire object”, see Table S1). In cases where the previous descriptions were sufficiently intuitive, we kept them in their original form (e.g., “Move closer”). We exclusively chose imperative paraphrases, as currently most of the established ape gesture uses resemble directives in human communication.

2.2 Creating the video gesture stimuli

When creating the gestures, the human signaller aimed to keep (as best as possible) all non-gesturing parts of her body neutral and similar across videos (e.g., keeping a neutral face to avoid potentially communicative facial expressions). The gesture actions were produced with chimpanzee expressions in mind; for example, chimpanzee hands typically include some flexion in the fingers and wrist as a neutral position.

Video recordings were created in the Socio-Cognitive Laboratory of the University of Oslo, which has four wall-mounted cameras. Both the signaller and the recipient were adult female researchers and were sitting on the couch engaged in reading prior to gesture production. Videos were cut to include only a few frames before the interaction started followed by the preparation and action stroke of the gesture (following Kendon, 2004); hold and recovery phases were excluded. In doing so, we also excluded any signs of the signaller waiting for a response, or any eventual response by the recipient (see also the similar *Minimum Action Unit* (MAU) termed for ape gestural research (Grund et al., 2023)). In this way, we provided the minimum information necessary to distinguish a gesture form, but no further information on the nature or success of the interaction between the two experimenters. No audio was provided with the video material, and participants were explicitly instructed that none was available.

2.3 Participants

The experiment was conducted as an online community-science experiment using the Gorilla.sc (www.gorilla.sc) platform (Anwyl-Irvine et al., 2020). Participants ($n = 300$) were recruited through various social media channels, mailing lists, and word of mouth; participation was voluntary, and participants were not paid. Participants were asked to select their birth year, so that we only collected data from participants over 18 years old—participants under 18 were able to access the study in game format (no data were collected). Ethical approval for this study was obtained in advance from the University of St Andrews University Teaching and Research Ethics Committee (approval code PS15109).

2.4 Procedure

Participation took place online and at the participants' own pace. Participants first read an information page and, if they chose to proceed, they then filled out a consent form and a short demographic questionnaire, which included asking for their age, gender (following Spiel, Haimson & Lottridge, 2019), and whether they had done the experiment before. The study was open for anyone who wished to partake, but as participant identification was anonymous, we used the self-reported information to exclude data of participants who: reported being younger than 18 years old or who had previously taken this experiment; or who at the

completion of the study did not fully complete the study questions or reported any within-experiment errors that could have impacted their results, for example video play-back errors.

Participants were presented with 10 trials. Each trial included a video of the gestural interaction, a humanoid “gesture-bot” illustration indicating the movement that they should attend to (Figure S1), and a choice of four possible responses. The videos showed a gesture form performed by one human experimenter to another, and were played once in real time, and once slowed to 50% speed. Participants were able to re-watch each video as often as needed. They were asked to choose the response that they thought most represented what the signaller wanted to communicate to the recipient. After 10 trials, participants were shown a final screen of their score (calculated as the correspondence of their answers to chimpanzee meanings) followed by a short debrief. All participants saw the same set of available responses for each gesture form; however, the presentation order of the gesture videos was randomised. In each trial of a Tight gesture (where there was only one correct response), the four available responses included the single “expected” response (i.e., the chimpanzee meaning, see Table S1) together with three “incorrect” distractor responses; in each trial with a Flexible gesture (where there were two correct meanings), the four available responses included the two “expected” responses and two “incorrect” distractor responses (Figure S1 illustrates the interface). All “incorrect” distractor responses were randomly selected from the set of other ape gesture responses used in the study. Once selected, the same distractor meanings, as well as the correct meaning(s), and the order in which they were presented were kept consistent across participants.

2.5 Analyses

We analysed $n = 3,000$ responses from $n = 300$ participants. We performed two sets of exact binomial tests: The first tested whether a single “most frequent” meaning was chosen more often than chance for each gesture form, and the second tested whether the chimpanzee meaning(s) for a gesture form were chosen more frequently than expected by chance. Confidence level was set to 95%, and the alternative hypothesis was one-sided (as we tested whether the most frequent response occurred at above chance level, rather than allowing it to vary in either direction). Statistical analyses were run in Rstudio 1.4.1103, running R version

4.0.3. Alpha was set at $\alpha = 0.05$ but following Bonferroni correction for multiple testing was adjusted to $\alpha = 0.005$ for each set of tests.

2.6 Hypotheses

For each of the ten gesture trials, the null hypothesis was that no consistent response would be assigned to the gesture across participants:

Experimental null hypothesis = there is no response option consistently associated with the gesture form. *Prediction*: responses are not significantly above chance level (25%)

This null hypothesis was rejected for a given gesture form when the most frequent response across all participants was above chance. If rejected, this would indicate that at least one meaning was more strongly associated with the gesture form across participants than the other meanings. This conclusion holds regardless of whether the most frequent response(s) correspond to the “expected” chimpanzee meaning(s), which was checked in a second step.

Correspondence hypothesis = the preferred response(s) for a given gesture form correspond to the established chimpanzee meaning(s) for that gesture form. *Prediction*: the chimpanzee meaning(s) for a gesture form are selected statistically above chance level (>25% for Tight, and >50% for Flexible).

Non-corresponding meaning hypothesis = the preferred response(s) converge on the same meaning (e.g., gesture form T is associated with response option A) that does not correspond to the “expected” response(s). *Prediction*: the most frequent response is selected statistically above chance level (>25% for Tight, and >50% for Flexible), and does not match the established chimpanzee meaning for that gesture form.

3. RESULTS

Participants selected one response significantly more frequently than would be expected by chance in nine of the ten gesture forms (Figure 2; Table 1).

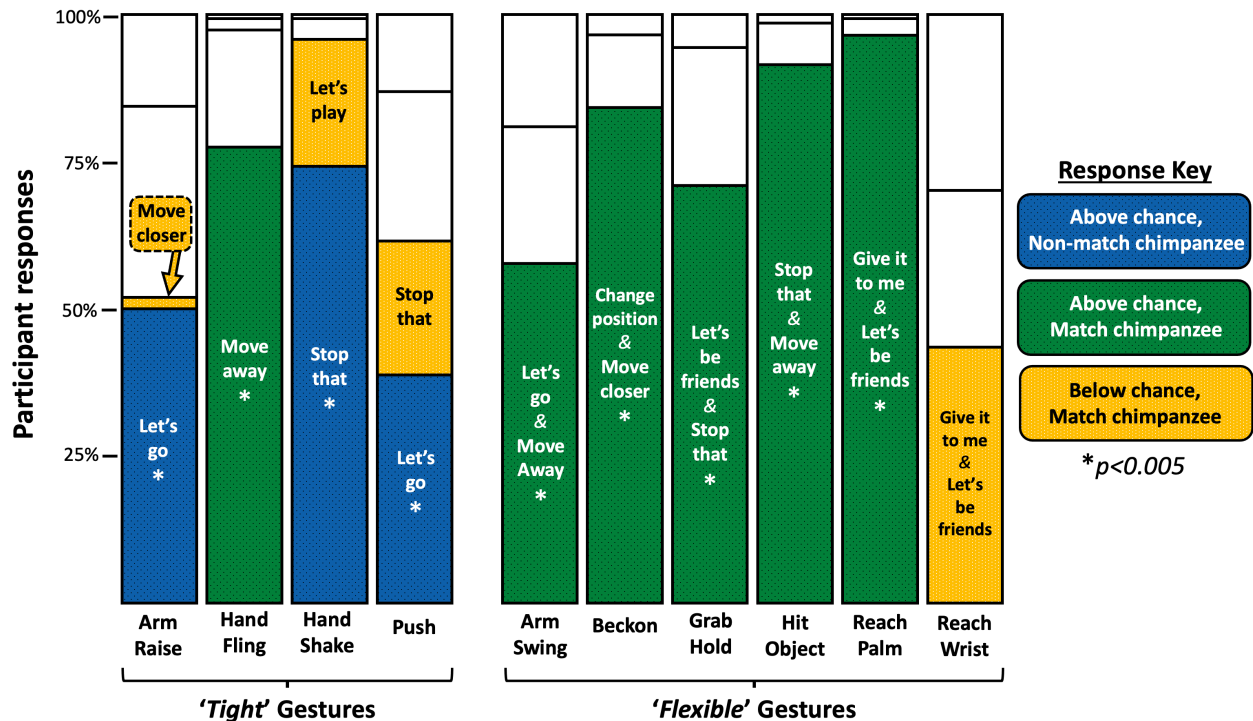


FIGURE 2. Proportional stacked histogram of participants responses per gesture. Blue bars indicate that participants selected a response significantly above chance and that differed from the chimpanzee usage of this gesture form. Green bars indicate that participants selected a response significantly above chance and that matched the chimpanzee usage of this gesture form. Yellow bars indicate a chimpanzee usage that was not selected at above chance levels for the given gesture form. White bars indicate a meaning that differed from chimpanzee usage and was not selected at above chance levels. Note that the first response listed for each Flexible gesture form was also the single most frequently selected response ($p < 0.005$). See Tables 1 and 2 for full results of all tests.

TABLE 1. Most frequent participant responses for each gesture form. ** indicates that participants selected the most frequent meaning significantly above chance (chance = 25% for all gestures; following Bonferroni corrections, $\alpha = 0.005$). The most frequent meanings selected may or may not match an established chimpanzee meaning. Bold text for responses in the centre column indicates where the most frequent response matched an established chimpanzee meaning.

Gesture form (<i>Tight or Flexible</i>)	Most frequent response (%)	Binomial tests: p-value 95% confidence intervals [LL, UL]
<i>Arm raise</i> (<i>Tight</i>)	“Let’s go” (50%)	**p<0.001 [0.451, 1.000]
<i>Arm swing</i> (<i>Flexible</i>)	“Let’s go” (50%)	**p<0.001 [0.454, 1.000]
<i>Beckon</i> (<i>Flexible</i>)	“Move Closer” (83%)	**p<0.001 [0.794, 1.000]
<i>Grab hold</i> (<i>Flexible</i>)	“Let’s be friends” (51%)	**p<0.001 [0.458, 1.000]
<i>Hand fling</i> (<i>Tight</i>)	“Move away” (77%)	**p<0.001 [0.730, 1.000]
<i>Hand shake</i> (<i>Tight</i>)	“Stop that” (74%)	**p<0.001 [0.695, 1.000]
<i>Hit object</i> (<i>Flexible</i>)	“Stop that” (91%)	**p<0.001 [0.874, 1.000]
<i>Push</i> (<i>Tight</i>)	“Let’s go” (39%)	**p<0.001 [0.340, 1.000]
<i>Reach palm</i> (<i>Flexible</i>)	“Give it to me” (86%)	**p<0.001 [0.819, 1.000]
<i>Reach wrist</i> (<i>Flexible</i>)	“Change position” (32%)	p=0.0055 [0.272, 1.000]

Across all answers, participants selected responses matching the chimpanzee meanings for each gesture form significantly more frequently than expected by chance (binomial $n = 0.568$, $p < 0.001$, LL = 0.553, UL = 1.000), and appear to do so to a greater extent in the six Flexible gesture trials

(binomial $n = 0.740$, $p < 0.001$, LL = 0.722, UL = 1.000) than the four Tight gesture trials (binomial $n = 0.309$, $p < 0.001$, LL = 0.287, UL = 1.000). Binomial tests on individual gesture forms revealed that participants selected the chimpanzee meaning significantly above chance in six of the ten gesture trials (Table 2): which included five Flexible gesture forms (*Arm swing*, *Beckon*, *Grab hold*, *Hit object*, *Reach palm*), and one Tight gesture form (*Hand fling*).

TABLE 2. Correspondence of participant responses to the established chimpanzee meanings. Responses for Flexible gestures forms were combined as a *Total* value as they both matched their use in chimpanzees. Binomial tests were used to check significant response selection above chance level (chance = 25% for Tight gestures forms, and 50% for Flexible gestures. ** indicates that participants selected the established chimpanzee gesture meanings significantly above chance (following Bonferroni corrections, $\alpha = 0.005$). Bold text for responses in the centre column indicates a chimpanzee meaning that matches the most frequent response for the gesture.

Gesture form (<i>Tight or Flexible</i>)	Response(s) of established chimpanzee meaning (%) <i>+ for Flexible forms: Total (%)</i>	Binomial tests: p-value 95% confidence intervals [LL, UL]
<i>Arm raise</i> (<i>Tight</i>)	“Move closer” (2%)	$p=1.0000$, [0.009, 1.000]
<i>Arm swing</i> (<i>Flexible</i>)	“Let’s go” (50.3%) + “Move away” (7.3%) = <i>Total</i> (57.7%)	** $p=0.0046$, [0.528, 1.000]
<i>Beckon</i> (<i>Flexible</i>)	“Move closer” (83.3%) + “Change position” (0.7%) = <i>Total</i> (84.0%)	** $p<0.001$, [0.801, 1.000]
<i>Grab hold</i> (<i>Flexible</i>)	“Stop that” (20.3%) + “Let’s be friends” (50.7%) = <i>Total</i> (71.0%)	** $p<0.001$, [0.663, 1.000]
<i>Hand fling</i> (<i>Tight</i>)	“Move away” (77.3%)	** $p<0.001$, [0.730, 1.000]

<i>Hand shake</i> (Tight)	“Let’s play” (21.7%)	p=0.9210, [0.178, 1.000]
<i>Hit object</i> (Flexible)	“Move away” (0.7%) + “Stop that” (90.7%) = <i>Total</i> (91.3%)	**p<0.001, [0.882, 1.000]
<i>Push</i> (Tight)	“Stop that” (22.7%)	p=0.8414, [0.187, 1.000]
<i>Reach palm</i> (Flexible)	“Give it to me” (85.7%) + “Let’s be friends” (10.7%) = <i>Total</i> (96.3%)	**p<0.001, [0.940, 1.000]
<i>Reach wrist</i> (Flexible)	“Let’s be friends” (17%) + “Give it to me” (26.7%) = <i>Total</i> (43.7%)	p = 0.9879, [0.389, 1.000]

4. DISCUSSION

In this study, we piloted a new inter-disciplinary method that employed recent findings and methods from great ape gesture research to investigate human intuitions about established chimpanzee gestural forms and meanings. Further exploration into the shared gestural features between humans and chimpanzees could help to unravel the origin of potential semantic universals that could have been crucial for the emergence of human language. We hypothesized that: If both the form of chimpanzee gestures and some abstract meaning component(s) associated with them are derived from traits present in a common ancestor with humans, then these gestural forms may have similar recognizable meanings for human adults, forming part of a universal “ape-typical” inventory of abstract meaning components that all human and nonhuman apes have access to.

Applying and refining the methodology of a recent online experiment developed to access understanding in language proficient humans of ape gesture form-meaning pairs produced by other apes (Graham & Hobaiter, 2023), we recreated these gestures in a human-human interaction. Study participants converged on a common response for nine of the ten “ape” gesture forms deployed in a naturalistic human interaction. The common meanings that they chose matched the established chimpanzee meanings in six of the ten gestures. This pattern suggests that humans recognise these as meaningful gesture units; they independently

agreed on common meanings communicated by the gestural forms, which often matched the same meaning in chimpanzees. As is the case in other apes, even where a gesture is most often used to communicate a single meaning, specificity varied. For the gesture forms with significant agreement across participants, participant agreement ranged from 39% (“Let’s go” meaning for *Push*) to 91% (“Stop that” meaning for *Hit Object*).

However, our results do not show gesture meanings shared across species for all gesture forms. The responses given in reaction to four of the ten gesture forms did not significantly correspond with their established chimpanzee gesture meanings. One gesture, *Reach Wrist*, did not exhibit a significantly most frequent response across participants, with participants’ responses similarly distributed across the four meaning options. A further three gesture forms (*Arm Raise*, *Hand Shake*, and *Push*) did exhibit a significantly most frequent response, indicating a shared inference about their meaning in humans, but this response did not match the established chimpanzee meaning (*non-corresponding meaning*). There are a number of reasons why convergence on a single meaning response may have occurred for all but one gesture form, and further testing is needed to disentangle them. It is possible that humans in general will converge on some common meaning(s) for any particular action, but our case of *Reach Wrist* shows that it is not always the case. We remain agnostic as to whether convergence on a shared meaning suggests that gestural form-meaning pairings are necessarily phylogenetically shaped (the phylogenetic gesture hypothesis), or whether shared patterns of action and meaning are individually acquired as a result of shared similarities in the physical structure of ape body plans and typical social interactions (the acquired gesture hypothesis). Similarly, we remain agnostic as to the possible fundamental properties of meaning in certain movements – i.e., whether gesture forms can be decomposed into meaningful parts. One approach to test the phylogenetic gesture hypothesis versus the acquired gesture hypothesis would be to explore whether humans are similarly skilled at decoding meaning in the gestures of other more distantly related species, such as elephants or corvids (compare Emery & Clayton, 2004; Smet & Byrne, 2020).

That the meanings of these gestures did not correspond to the chimpanzee meanings may reflect the importance of contextual cues in interpreting gesture. All of the gesture form-meaning pairs selected were ones that could be plausibly produced in an adult-adult human interaction. However, our current methods for specifying meaning in ape gesture require

further development. For example, presently it would be difficult to disentangle whether a flexible gesture had two distinct lexical meanings (such as the meanings captured by the paraphrases “Move closer” and “Move away”) or if it communicated a single, more general meaning (such as “Move yourself”) that is further specified by the recipient given the situational context (See Patel-Grosz, 2023 for a linguistic approach to this question). The significance of context to disambiguate meaning in gesture is increasingly supported (e.g., humans: Morrison, 2020; bonobos: Graham, Furuichi & Byrne, 2020). While interpretations of our findings are relatively speculative at this stage, we aim to conduct future studies that directly test the role of context in gestural interpretation.

The gestures included in our experiment were not intended to reproduce gesture forms known to exist in adult humans (though they may unintentionally resemble some such gestures), nor were they spontaneously produced by adult humans in natural conversation; rather, they were controlled re-enactments of established chimpanzee gestures produced as if they were human gestures. If human participants were asked to interpret the meaning of a gesture produced by a chimpanzee, as in Graham and Hobaiter (2023), we cannot know if the participants tried to “guess” what the chimpanzee is trying to communicate based on their knowledge of chimpanzee behaviour (thus assuming the perspective of the chimpanzee), or if they are interpreting the gesture’s meaning from the situational context, as opposed to treating the gesture as a species-independent gesture that *could* be used by a human. In videos of naturalistic gesture use in other apes, there are many uncontrolled confounds that make it difficult to discern the extent to which human observers are able to extract information on the gestural meaning based on the physical expression of the gesture; as opposed to the socio-ecological context, or other accompanying signals (such as facial expressions, vocalisations, body position, etc.). To help control other potential confounding variables, our videos were generated in a highly constrained setting: the signaller and recipient started each video sat in the same position and location, the signaller produced each gesture while suppressing other accompanying signals, and the recipient consistently reacted to each produced gesture. Thus, we were able to refine our investigation to how participants understood the relevant morphological actions of each gestural form without additional contextual information.

We employed a novel experimental method recently developed to test human understanding of chimpanzee gestures (Graham & Hobaiter, 2023), here performed in a

human-human interaction. We will continue to adapt this study design to test a greater variety of gestures, meanings, and contexts. Nonetheless, our current experiment represents a crucial proof of concept, and our results remain useful for several key reasons. Firstly, our approach provided a particularly challenging test of our hypothesis, presenting minimal gestural information; tight control of situational and interactional context; and inclusion of Flexible gesture forms that can – in other apes – be deployed across multiple meanings. The difficulty of the task was reflected in feedback from participants (through the experiment’s comment section and via email).

A non-trivial question is to what extent we can be certain that a human expert can recreate a chimpanzee’s gesture in a way that would be recognized by a chimpanzee. While human and chimpanzee vocal anatomy is substantially different (Nishimura et al., 2022), the physiology (i.e., bones, joints, muscles) of the limbs used by humans and chimpanzees to produce gestures is nearly identical in configuration. As a result, while the authentic reproduction of chimpanzee vocal signals by a human would not be possible, authentic reproduction of gestures is much more feasible. Nevertheless, the human expert might fail to integrate some important component of a chimpanzee’s gesture, such as a slight hand movement, elbow angle, or specific finger position. However, as chimpanzee gestures are not identically produced in every instance, their gesturing naturally contains temporal and physical variability with regards to properties such as: extension, flexion, orientation etc. (Grund et al., 2023; see also: www.greatapedictionary.com). The parts kept constant are relatively coarse and there is no evidence that finely nuanced differences as listed above (e.g., finger position) would change the meaning of a gesture in an ape. Indeed, these gestures need to be understandable to other chimpanzees in a visually complex environment of dark, dense foliage in the wild, and thus need to be robust to subtle variation in form.

By only showing participants the preparation and action stroke phase of each gesture (i.e., excluding any hold, repetition, or recovery; cf. Kendon, 2004; Grund et al., 2023), we provided the minimal possible information on the gesture form, making the detection of differences between similar gesture forms potentially more challenging. For example, the distinction between *Hand Fling* and *Hand Shake* may be more difficult when a participant only observes the first back and forth movement without repetition (see Figures S2 & S3). This natural ambiguity in gestural forms may underlie some of our findings, for example in

the *Hand Shake* gesture form yielding a consistent (but unexpected) preference for the meaning “Stop that” (74%). It is plausible that participants interpreted the abbreviated *Hand Shake* similarly to a *Hand Fling*, which participants typically interpreted with the expected chimpanzee meaning “Move away” (77%). Moreover, *Hand Fling* is a Tight gesture, and its single correct meaning may be more robust to misinterpretation compared to the two correct meanings of the Flexible gesture, *Hand Shake*. Future studies should present different phases of gestural movements to tease apart how participants discriminate similar gesture forms.

By using human actors to perform ape gestures, we could control factors that are normally present in natural interactions and that may impact how gestures are understood. We excluded other accompanying signals (e.g., vocalisations or facial expressions) and kept situational and interactive context consistent across trials. Our videos did not include any response waiting or an outcome to the signal, which created a 'minimally-informative' environment for the interpretation of gestural meaning. Furthermore, some gestural meanings are dependent on the previous behaviour of the signaller and recipient – for example, chimpanzees use *Push* gesture forms to communicate “Stop that”, which presupposes a previous action on the part of the recipient (i.e., “*Stop that*” presupposes *you were doing something before*). In our experiment, the video started with the recipient not engaged in any visible interaction with the signaller before the gesture – they were sitting reading on the couch. While participants could take “Stop that” to indicate “Stop reading”, this may be a less plausible meaning given the benign nature of reading as an activity. However, where participants selected meanings that fit less well into the provided video context, it is possible that they either ignored the immediate context or that they prioritised a meaning they felt best fit with the gesture’s form over contextual cues. Future research could investigate how presenting participants with different behavioural contexts before the gesture is produced may impact interpretation.

Within the large repertoires of great ape gestures (~80 distinct gesture forms; Byrne et al., 2017), we selected only 10 gesture forms based on their plausible production in typical human interactions, excluding forms such as *Pirouette* and *Big loud scratch*. While doing so limited our exploration of the full gestural repertoire, we wanted to rule out unsuccessful interpretations as a result of presenting participants with inappropriate gestures and meanings – a non-negligible confound. Now that we have established that the method works in principle

to detect human understanding of great ape gestures, future investigation could explore a wider range of gesture forms, such as testing all manual gestures.

We also limited our responses to meanings that have been established for chimpanzees, excluding our other closest living relative, the bonobo. While chimpanzees and bonobos share substantial overlap in their gesture forms and meanings, there remain some important differences in these closely related species (Graham et al., 2018). Given that both species are equally related to humans (e.g., Fischer et al., 2006), the inclusion of more gestural form-meaning pairings from bonobos may further expand our ability to detect points of gestural overlap (Kersken et al., 2019). It will also be important to incorporate further research into ape gesture use across each species more broadly, including gorillas and orangutans, and to examine sub-species and population level overlap or variation.

Through interdisciplinary collaboration between primatologists and linguists, our study pilots a new framework for comparative great ape gesture research. We test the idea that there may be shared understanding of gestural form-meaning pairings that are accessible to humans as well as other apes. It remains to be established whether these represent true ape “universal” gestures – for example, through the application of ape methods to the study of human gesture production. Potential meaning components would naturally be highly abstract, such as a notion of *encouragement* (which could form the core of a gesture that means “Give it to me” or a gesture that means “Move closer”) or a notion of *discouragement* (which could form the core of a gesture meaning “Stop that” or “Move away”). Our participants converged on a common meaning in nine out of ten gesture forms, and these corresponded with the comparable chimpanzee meaning in six cases. We demonstrate further “proof of concept” that this new video-based forced-choice approach can be extended to human-human interactions when testing the shared evolutionary roots of “ape” gesture. By finding that humans share their understanding of some gesture forms with chimpanzees, our results support the hypothesis of an underlying phylogenetically-shared system of gesture that spans across ape species. We propose that future use and improvement of this experimental framework can help to address questions investigating the deep evolutionary origins of ape gesture; and uncovering potential universals of this shared system of form-meaning pairings may reveal the deep evolutionary roots of language.

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Supplemental Materials

The ten chimpanzee gestures with established meanings (Table S1), are based on those established in Hobaiter and Byrne's (2014) and updated using the same approach but including new (unpublished) data.

TABLE S1. Selection of 10 gesture forms and meanings. In cells with two meanings (for so-called "Flexible gesture forms"), both are compatible meaning pairs with the gesture form; the one listed first in such a cell is more frequent than the one listed second.

Gesture Form	Original chimpanzee meanings	Translations to human-appropriate
<i>Arm Raise</i>	"Move closer"	"Move closer"
<i>Arm Swing</i>	"Follow", "Move away"	"Let's go", "Move away"
<i>Beckon</i>	"Move closer", "Reposition yourself"	"Move closer", "Change position"
<i>Grab Hold</i>	"Stop that", "Affiliation"	"Stop that", "Let's be friends"
<i>Hand Fling</i>	"Move away"	"Move away"
<i>Hand Shake</i>	"Start play"	"Let's play"
<i>Hit Object</i>	"Move away", "Stop that"	"Move away", "Stop that"
<i>Push</i>	"Stop that"	"Stop that"
<i>Reach Palm</i>	"Acquire object", "Affiliation"	"Give it to me", "Let's be friends"
<i>Reach Wrist</i>	"Affiliation", "Acquire object"	"Let's be friends", "Give it to me"

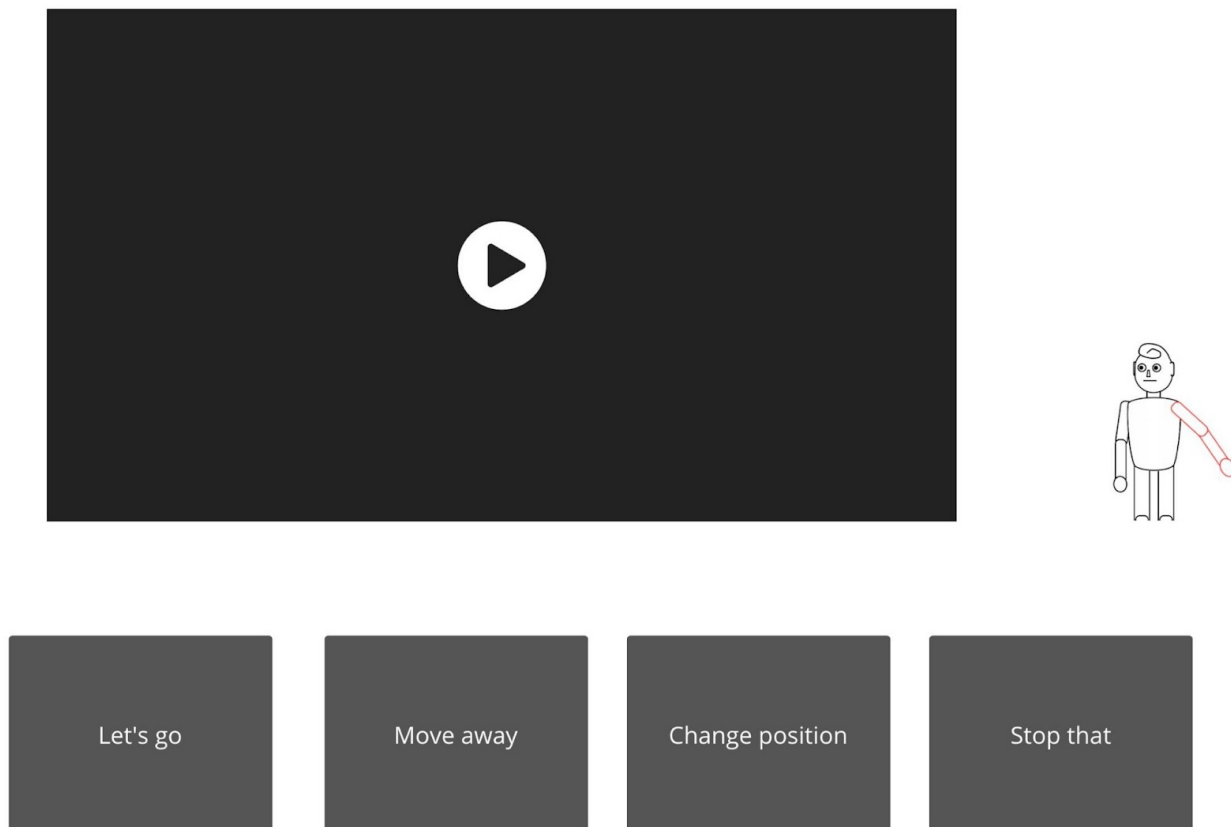


FIGURE S1. Experimental interface seen by participants.

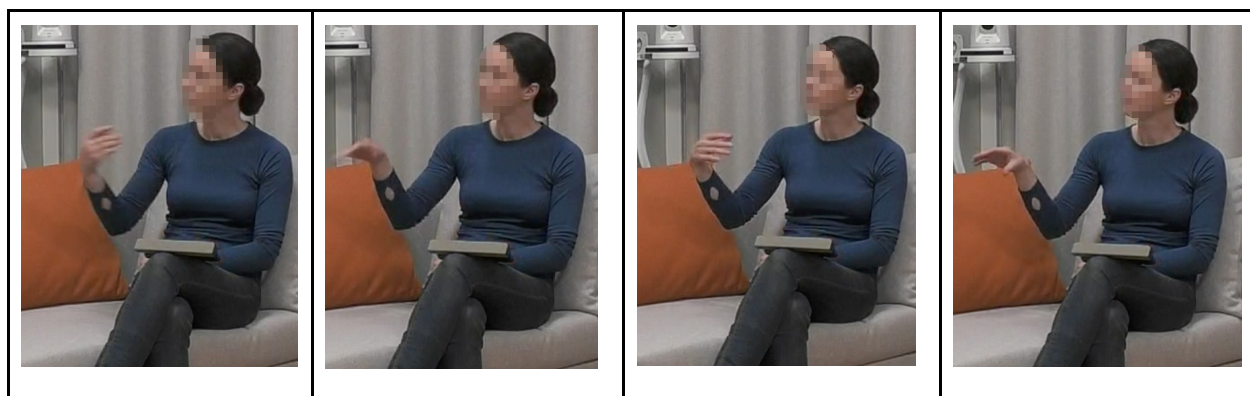


FIGURE S2. Four stills to illustrate the *Hand Shake* gesture.



FIGURE S3. Three stills to illustrate the *Hand Fling* gesture.