

Content biases in three phases of cultural transmission: A review

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Abstract

Cultural evolution theory proposes that information transmitted through social learning is not transmitted indiscriminately but is instead biased by heuristics and mechanisms which increase the likelihood that individuals will copy particular cultural traits based on their inherent properties (content biases) and copy the cultural traits of particular models, or under particular circumstances (context biases). Recent research suggests that content biases are as important, or more important, than context biases in the selection and faithful transmission of cultural traits. Here, evidence for biases for emotive, social, threat-related, stereotype consistent and counterintuitive content is reviewed, focusing on how these biases may operate across three phases of transmission: choose-to-receive, encode-and-retrieve, and choose-to-transmit. Support for some biases primarily functioning as biases of attention and memory, while others primarily function as biases of selection to share with others, and the implications for this in wider cultural evolution is discussed. Ultimately, a more consistent approach to examining content biases, and greater engagement with wider literature, is required for clear conclusions about their mechanism and potential differences across the three phases of transmission.

A key premise of cultural evolution is that information is not transmitted indiscriminately but is influenced by mechanisms which bias this transmission in certain directions (Boyd & Richerson; Henrich & McElreath, 2003; Laland, 2004). These transmission biases (also referred to as ‘social learning strategies’) increase the likelihood that individuals will copy particular behaviours (content biases), and copy the behaviours of specific models, under particular circumstances (context biases) (see Kendal et al 2018 for a review). Content biases (also referred to as ‘direct’ biases) lead individuals towards preferentially copying or learning a behaviour or trait based on its inherent characteristics, rather than the characteristics of the model or the context in which the transmission takes place. This may be related to the effectiveness of that behaviour: a behaviour which produces a greater payoff is more likely to be copied and transmitted (payoff bias, see Kendal et al., 2009; Vale et al., 2017; van Leeuwen et al., 2013; van Leeuwen & Call, 2017). Other content biases relate to the nature of what is being transmitted, seemingly (or at least not overtly) unrelated to the payoff of that behaviour. These include biases for content which is emotionally evocative (emotional bias, e.g. Kashima et al., 2020), relevant to threats and survival (threat bias, e.g. Blaine & Boyer, 2018), related to social interaction (social bias, e.g. Mesoudi et al., 2008), consistent with cultural stereotypes or expectations (stereotype consistency bias, e.g. Lyons & Kashima, 2006), and is minimally counterintuitive (MCI bias, e.g., Norenzayan, 2006).

To date, cultural evolution and social learning has primarily focused on context biases, with relatively less attention being paid to the role of content biases in the evolution of human culture, and content biases have largely been studied independently of context biases. Recent research, however, suggests that, when examined together, content biases play as important, or a more important role in social transmission than context biases. Prestige bias, where models of high social position, reputation, and knowledge are preferentially copied (Berl et al., 2020), is one of the most cited transmission biases (Jiménez & Mesoudi, 2019) but has been found to be less influential on the transmission of narratives than social, threat and negative emotional, and MCI content biases (Berl et al., 2021). Content biases have also been found to be equivalent to, or more important than context biases in studies of the selection of inspirational quotes (Acerbi & Tehrani, 2018) and the dissemination of conspiracy theories (Youngblood et al., 2021).

Research directly examining content biases in social transmission has typically focused on what content is preserved in linear, recall-based transmission chain (also referred

to as diffusion, or serial reproduction chain) experiments (see Mesoudi, 2007) and has rarely directly addressed the mechanisms involved in preserving content in wider culture, seemingly assuming memory to be central to this process. While one might consider selection as part of this process in terms of what content is preserved in memory, it does not directly address the role of selection in transmission as there is no element of choice in what is received, nor in what is transmitted. In critique of this, Eriksson and Coultas (2014) proposed three distinct transmission phases: choose-to-receive, encode-and-retrieve, and choose-to-transmit. Choose-to-receive refers to attending to and selecting material; encode-and-retrieve refers to the process of material being encoded and later retrieved from memory; and choose-to-transmit refers to the selection of material to transmit to another or others. These three phases reflect early distinctions made by Allport and Postman (1947) in the processes of rumour transmission: perceiving by the senses, remembering what was perceived, and reporting that perception to others.

Here, research examining content biases in social transmission is reviewed, concentrating on emotional bias, threat bias, social bias, stereotype consistency bias and MCI bias. This selection of biases is informed by studies within cultural evolution which have considered the role of multiple biases (Acerbi, 2019; Berl et al, 2020; Stubbersfield et al, 2017) and reviews of social learning biases and cultural evolution theory (Kendall et al, 2018; Mesoudi, 2016, 2021). While there is some variation in coverage across these sources, all include emotional and social bias, and the majority include the other biases. The exception being stereotype consistency bias, only discussed in Stubbersfield et al (2017) and Mesoudi (2016) (in the context of schematisation). It was felt that, while not considered in the majority of sources, the level and history of research dedicated to this topic in psychology, and its link to wider discussions of schema, warranted its inclusion.

With consideration for the three phases approach, the review is organised by phase rather than by bias. In considering the three phases, the review goes beyond literature that explicitly examines content biases through cultural evolution theory and includes relevant literature from the psychology of attention, memory, and communication. In doing so, valuable insights into the cognitive mechanisms involved in the expression of these biases are gained. This three-phases focus has the benefit of enhancing our understanding of inconsistencies in the existing research and is particularly relevant to understanding cultural transmission in contemporary culture, where electronic communication allows for the easy transmission of information without any reliance on recall. This has broad implications for

our understanding of biases in cultural transmission, predictions of cultural evolution in different contexts, and the assumptions of models of cultural evolution.

Choose-to-receive

The choose-to-receive phase of transmission involves an individual attending to and selecting to receive information. Content biases in this phase increase the likelihood that content will draw attention and interest. Research from the psychology of attention is relevant to this phase as selection is considered central to attention (Yiend, 2010). When presented with competing stimuli, our processing system displays biases as a result of both bottom-up and top-down processes (Desimone & Duncan, 1995; Yiend, 2010). Rumour psychology has recognised the importance of this phase of transmission, arguing that the cognitive mechanisms of attentional narrowing and perceptual bias play an important role in the transmission of rumours (DiFonzo & Bordia, 2007).

Cultural psychology has demonstrated differences in attentional focus between people from Western cultures (typically the USA) and people from East Asian cultures. These studies have found that Western participants typically attend more to focal objects, and self-relevant content, compared to East Asian participants who attend more to the background context, the relationships between focal objects and background, and group-relevant content (Gutchess & Inneck, 2009; Masuda & Nisbett, 2001; Nisbett & Masuda, 2003). While it has not been examined if this produces differences in cultural transmission, cross-cultural differences in attention such as this may result in differences in the expression of content biases in this phase.

The broad and longstanding interest in attention has generated a large body of literature beyond the scope of this review, however, relevant work is included to highlight their relevance to content biases and wider cultural evolution theory.

Emotion bias

Eriksson and Coultas (2014) tested for a disgust bias in this phase by having participants select an urban legend to read from headlines reflecting those legends. They found that more disgusting urban legends were more likely to be selected. Similarly, Trussler and Soroka (2014) found that participants in a study of news consumption were more interested in reading negatively valenced news. Beyond these studies, however, emotional bias in the choose-to-receive phase of transmission has not been explicitly examined.

With regards to emotion biases in attention, research has adopted a dimensional approach, considering the dimensions of valence (positive to negative) and arousal (low to high) (Lang et al, 1993; Russel, 1980, 2003; Russell & Barrett, 1999). Research suggests that human cognitive systems produce an attentional bias towards emotional stimuli over neutral stimuli (see Dolcos et al., 2020, Fenske & Raymond, 2006, Vuilleumier, 2005, and Yiend, 2010 for reviews, and Kashima, 2020 for review in the context of cultural transmission). Both pleasant and unpleasant emotional stimuli increase selective orientation compared to neutral scenes (Fernández-Martín & Calvo, 2015) and abstract emotional images are prioritised in processing (Pilarczyk & Kuniecki, 2014). Eye movement tracking studies show a bias for emotional stimuli in fixation (Alpers, 2008; Calvo & Lang, 2004; Nummenmaa et al., 2006) and in saccades (rapid eye movements) (see Mulckhuysen, 2018 for review). Neuroimaging studies also suggest an emotional bias in attention (e.g., Whalen et al., 1998; Vuilleumier, et al., 2001). However, this attentional bias for emotional stimuli is influenced by variation in individual differences in gender, personality, and age (MacLeod & Matthews, 1991; Matthews & Milroy, 1994). For example, older adults show a positivity bias in attention (Knight et al., 2007; Mather & Carstensen, 2003), and women show greater sensitivity to and attention towards emotional stimuli than men, especially for negative stimuli (Collignon et al., 2010; Hall & Matsumoto, 2004).

Further, there is evidence that content evoking negative sentiment may have a greater advantage in attention than positive content (see Baumeister et al., 2001; Rozin & Royzman, 2001 for reviews of general negativity bias in psychology). Attention studies suggest attentional bias towards negative stimuli (especially anger and fear-relevant) over neutral stimuli (see Frischen et al, 2008 for review, but see Tipples et al, 2002), and particularly towards disgust-relevant stimuli (van Hoof et al., 2013, 2014; Xu et al., 2016). This includes

evidence from eye-movement tracking studies that unpleasant images receive more attention (McSorley & van Reekum, 2013). Visual search tasks generally show that negative content is found more quickly and efficiently than neutral content (Yiend, 2010). Much of the research on negative valence and attention uses facial stimuli which may have limited relevance to cultural transmission, however, it has been found that negatively framed statements are similarly processed more quickly than neutral statements (Hilbig, 2009, 2011, 2012) and impression formation also displays negativity bias, with negative content holding more influence over impression formation than positive information (Peeters & Czapinski, 1990). There is limited evidence of cross-cultural differences in attention towards negative and positive stimuli: Grossman et al., (2012) found that Russian participants displayed greater attentional bias towards negative stimuli than American participants, indicating that culture may influence the salience of negative emotional content.

That emotional content, especially negative emotional content is more likely to draw attention does not necessarily mean it will be selected to be received; while quick and automatic attention will grant some advantage initially, it might be that people quickly choose to avert their attention away from unpleasant stimuli. It is argued that this attentional bias is an evolved response as the prioritisation of emotional stimuli is evolutionary adaptive (Mulckhuyse, 2018; Pilarczyk & Kuniecki, 2014), as such, this could drive prioritised processing so these stimuli can be more efficiently avoided, rather than engaged with (at least in the case of negatively valenced stimuli). However, it has been demonstrated that negatively framed statements are considered more credible (Fessler, 2019; Fessler et al., 2014), plausibly leading to increased selection within certain contexts.

Threat bias

It is generally understood that human attention is biased towards threatening visual stimuli (see Browning & Harmer, 2012; Yiend, 2010), and that this is an evolved response as being able to efficiently process threats in our environment is beneficial (Makovski et al., 2020; McSorley & van Reekum, 2013). Research on emotion in attention often elicits an emotional response through threat-relevant stimuli and, in general, biologically prepared threat stimuli (e.g., stimuli such as spiders or snakes rather than acquired fear stimuli such as weapons) have increased salience (Yiend, 2010), suggesting that some forms of threat

generate greater attention than other threats. While there appears to be a general attentional bias towards threatening stimuli, research also suggests significant individual variation, for example attentional bias for threatening stimuli is higher in 'fearful' individuals (Öhman & Mineka, 2001; Mineka & Öhman, 2002). Further, research on morbid curiosity suggests that some individuals are more inclined than others to seek out threat-relevant content (Scrivner, 2021b) and that this impacts on their media preferences, with more morbidly curious individuals more likely to choose to receive threat-related media, such as horror, and thrillers (Scrivner, 2021a).

Further, information about threats and hazards is more likely to be believed than information about benefits (Fessler, 2019; Fessler et al., 2014) which may plausibly increase selection. This has been shown to be dependent on beliefs about the world, as those who believe the world to be a dangerous place show a greater degree of threat-related credulity than those who believe it is safer (Fessler et al., 2017). Threat-related content may also interact with how the source of information is viewed. Sources of threat-related information about both situations and products are judged to be more competent than sources of equivalent information with no mention of threat (Boyer & Parren, 2015), again, plausibly increasing the likelihood that threat-related information will be selected. In one of the few studies to directly test for threat bias in the choose-to-receive phase of transmission, Stubbersfield et al. (2015) had participants rank headlines reflecting different urban legends in order of their preference to read them and found no advantage for threat-related information over social information. Although it should be noted that there was no comparison to control material, as such it cannot be concluded whether threat-related information would have an advantage over neutral information or not in this transmission phase from that study.

Social bias

It is argued that, as a result of human intelligence evolving in response to the challenges of living in complex social groups (Byrne & Whiten, 1990; Dunbar, 1998, 2003), humans will preferentially attend to content about the social relationships of third parties (Mesoudi et al., 2006). However, there has been little direct examination of social bias in the choose-to-receive phase of transmission. Relevant work comes from moral information in

impression formation, as moral information about a person is typically understood to be whether they are *socially* good or bad (Wojciszke et al., 1998). Research has found that people respond faster to person-related words from the moral domain (Ybarra et al., 2001), spontaneously categorise others using morality rather than competence (van Leeuwen et al., 2012), and demonstrate greater interest in information about the morality of another person compared to information about their competence (Wojciszke et al., 1998). This suggests a content bias for social information in choose-to-receive, at least within the context of information about other people. As mentioned earlier, in one of the few studies to directly test for social bias in the choose-to-receive phase of transmission, no advantage was found for social information over threat-related information (Stubbersfield et al., 2015).

Stereotype consistency bias

While no research has directly examined stereotype consistency bias in the choose-to-receive phase of transmission, research from rumour psychology has long identified that perceptual bias (i.e., the selective perception or interpretation of content to cohere to existing schemas) plays an important role in the transmission of rumours (e.g., Knapp, 1944; Turner, 1993).

Research related to attention and selection of surprising content can also be considered relevant, as surprise is often defined as a response to schema incongruity (Noordewier & Breugelmans, 2013; Schützwohl, 1998). Due to the association between surprise and attention (e.g., Browning & Harmer, 2012; Horstmann, 2002, 2015; Itti & Baldi, 2009; Loewenstein, 2019; Russell & Barrett, 1999; Schützwohl, 1998) we might expect that content which is *inconsistent* with stereotypes, and therefore surprising, would be advantaged in this stage of transmission (but see Rungratsameetaweemana & Serences, 2019 which suggests the association between attention and surprise is not fully understood). However, another well supported finding within psychology is confirmation bias, which suggests that people *seek out* information which confirms existing beliefs and expectations (Nickerson, 1998). Given this, we might expect stereotype consistent information to be advantaged at this stage of transmission. In either case, the extent to which cultural stereotypes are held to be true will play a vital role in whether stereotype consistent content is advantaged or disadvantaged during this phase.

Discussion and conclusions

The research reviewed here suggests that several content biases are expressed in the choose-to-receive phase of transmission. More arousing, emotional content is more likely to be attended to and selected, with some evidence for a negativity bias, especially for visual stimuli. There is also evidence for a threat bias in attention, but this is subject to significant individual variation and there is limited evidence that it may be less influential than social content in this phase. The evidence for stereotype consistency bias is inconsistent, as surprising stereotype inconsistent content appears to garner more attention, however, individuals may also seek out content which is consistent with existing schema, including stereotypes.

Encode-and-retrieve

The encode-and-retrieve phase of transmission involves an individual encoding information content in memory and subsequently retrieving that information in recall. Content biases in this phase increase the likelihood that content will be accurately encoded and later retrieved, and plausibly may transform content in the direction of the bias (see Bebbington et al., 2017, which found the negative transformation of ambiguous information). Research testing for content biases in social transmission commonly involves this phase, as material is commonly reproduced from memory in transmission experiments. Individual memory studies are also relevant. The encoding of information in memory and subsequent retrieval has been a topic of interest in psychology for decades generating an extensive body of literature that is beyond the scope of this review, however, relevant work is included to highlight the relevance of individual memory studies to this phase of transmission.

Emotion bias

It is established that emotion plays an important role in recall-based cultural transmission (see Kashima et al., 2020 for review). As in attention research, research

examining emotion and memory also adopts a dimensional approach (arousal and valence). Research suggests that emotionally arousing stimuli are better encoded in memory than neutral stimuli (see Dolcos et al., 2020, Kensinger & Schacter, 2008, LaBar & Cabeza, 2006, and Levine & Pizarro, 2004 for reviews). This effect is thought to be spontaneous (Kissler et al., 2007) and related to activation of noradrenergic transmission (Cahill, et al., 1994; de Quervain, et al., 2007) and increased recruitment of the amygdala-hippocampus complex (Phelps, 2004). Increasing arousal during exposure can also enhance the memory of neutral stimuli (Anderson et al., 2006a; Buchanan and Lohvallo, 2001; Ventura-Bort et al., 2016a; Ventura-Bort et al., 2016b). Despite this strong association, emotional memories are not indelible, and there is a lack of clarity regarding the role of valence, motivation, and differences between discrete emotions in memory (Levine & Pizarro, 2004).

Some researchers of memory have criticised the concept of ‘emotional arousal’ as excessively broad and producing a constrained understanding of emotion and memory, and the neglect of the role of discrete emotions in memory (see Feldman & Waller, 1962; Levine & Pizarro, 2004; Neiss, 1988). Work examining differences in memory between discrete emotions has found disgust-related images to be better remembered than fear-related images despite similar levels of valence and arousal (Chapman et al., 2013). A specific advantage for disgust has been found in memory (Chapman, 2018; Charash & McKay, 2002; Croucher et al., 2011; Ferré et al., 2018; Marchewka et al., 2011). In recall-based transmission, Eriksson and Coultas (2014) similarly found an advantage for disgust, finding that more disgusting urban legends had an advantage over less disgusting versions in a recall-based transmission chain, although this result was not found in a second study testing recall in an Indian sample (Eriksson et al., 2016). Another discrete emotion found to enhance recall is surprise, likely as a result of surprise being associated with increased arousal (Bradley et al, 1992; Loewenstein, 2019), attention, and engagement (Browning & Harmer, 2012; Horstmann, 2002; Itti & Baldi, 2009; Loewenstein, 2019; Russell & Barrett, 1999; Schützwohl, 1998). However, Stubbersfield et al. (2017a) compared the recall-based transmission of urban legends eliciting different discrete emotions at different levels of arousal and found that faithful transmission was predicted by arousal rather than specific, discrete emotions (including disgust).

Regarding valence, while not entirely consistent across domains, it is also argued that human memory is biased towards content with a negative emotional valence (Baumeister et al., 2001; Rozin & Royzman, 2001). Negative stimuli are remembered better than neutral or positive stimuli (see Kensinger, 2007 for review), and, similarly to attention, this is argued to

be the result of the adaptive value of prioritising negatively valenced experiences in memory (Boğa et al., 2021). The potential advantage for negative emotional content in memory is largely reflected in recall-based transmission studies. Using a recall-based transmission chain design, Bebbington et al. (2017) found that negative content is more faithfully transmitted than positive content. In a naturalistic study, Walker and Blaine (1991) seeded positive and negative rumours in an American college campus and found that the negative rumours spread more widely than the positive one (although while this was recall-based transmission, other phases of transmission likely played a significant role in the relative success of the rumours). In a transmission chain study designed to compare the simultaneous effects of prestige bias (using models with high- or low-prestige regional accents) and the presence of different types of narrative content, Berl et al. (2021) found negative content to be more influential than prestige

As in attention, individual variation has been found in studies of emotion and memory. Older adults appear to display positivity bias in memory (e.g., Bruno et al., 2014; Charles et al., 2003; Kennedy et al., 2004; Mather, 2006; Mather & Knight, 2005; Mikels et al., 2005; Reed et al., 2014, but see Allen et al., 2019; Kapucu et al., 2008 for no positivity bias in recognition memory) and women recall more emotional memories than men (Davis, 1999; Seidlitz & Diener, 1998), with gender differences in memory possibly explained by gender-specific societal expectations (Cahill et al., 2004).

Threat bias

Just as human attention is attuned towards potential hazards, it is argued that threat-related information is also be more memorable than other information. This is supported by Makovski et al. (2020), who found, in a series of experiments, that overall memory was enhanced by the presence of threatening images in the same display. Much of the research in this area has been conducted by Nairne and colleagues, who argue that the encoding and retrieval of information is tuned towards survival and have demonstrated that survival processing (where participants rate the relevance of words to their survival in a foreign grassland; then recall the list of words or recognise the words from a list) produces better recall and recognition memory than other processing techniques known to produce enhanced recall (such as rating the pleasantness of words) (Nairne et al., 2007; Nairne & Pandeirada,

2008; Nairne et al., 2019). Others have replicated these results with pictures rather than words (Otgaar et al., 2010), in a contamination context (Bonin et al., 2019), and when controlling for arousal and novelty (Kang et al., 2008). However, the survival processing effect is not found in an alternative, more modern imagined scenario (Weinstein et al., 2008), and is limited to certain types of stimuli (Kazanas & Altarriba, 2015). A systematic review of the survival processing literature found support for the survival processing effect being the result of survival threat (Tay et al., 2019). Threat-related content is also faithfully transmitted along recall-based transmission chains (Moussaïd et al., 2015), although less well than social information (Stubbersfield et al., 2015), but may play a more important role in faithful transmission than prestige bias (Berl et al., 2021).

Social bias

In addition to preferential attention, it is argued that social information should be better remembered than equivalent non-social information (see Mesoudi et al., 2006). Providing a social context as a link has been shown to improve the individual recall of vignettes (Owens et al., 1979) and paragraphs containing social information are better remembered by both individuals and groups than paragraphs containing no social information (Reysen et al., 2011). In addition to individual memory, social bias has been demonstrated in recall-based transmission, with social information being transmitted in greater quantity and with greater accuracy than equivalent non-social information (Mesoudi et al., 2006), and threat-related information (Stubbersfield et al., 2015). Social bias has also been demonstrated in the recall and transmission of political information (Aarøe & Petersen, 2018), in a more naturalistic transmission setting with children (McGuigan & Cubillo, 2013), and has been found to have a stronger effect than prestige bias on faithful transmission (Berl et al., 2021).

Stereotype consistency bias

Evidence for stereotype consistency bias in individual memory and recall-based transmission is inconsistent but suggests a small advantage for stereotype-inconsistent

content in individual memory. One meta-analysis found a small recall advantage for stereotype-consistent content over stereotype-inconsistent content (Fyock & Stangor, 1994). However, decades of research has found some advantage for expectation-violating or schema inconsistent content in memory (e.g., Bartlett, 1932; Jacoby & Craik, 1979; Schmidt, 1985, 1991; Smith & Hunt, 2000; Stangor & McMillan, 1992) and other meta-analyses of experiments investigating the influence of social expectations and schema on memory found a slight advantage for schema-inconsistent information over schema-consistent information (Rojahn & Pettigrew, 1992) and for expectancy-incongruent information over expectancy-congruent information (Stangor & McMillan, 1992). Rojahn and Pettigrew (1992) conclude that “the imperviousness of stereotypes to change must be sought in contextual and motivational factors rather than in alleged universal memory biases” (p.99). Porubanova et al. (2014) found that concepts which violate cultural expectations are better remembered than concepts which violate ontological expectations, especially when the concepts were related to agents, arguing that this is a result of the evolutionary salience of this content. As stereotypes represent cultural expectations related to agents, we might expect violations of them to be advantaged in individual memory compared to violations of expectations related to other, non-social, categories.

There has been a longstanding interest in psychology for examining the recall-based transmission of stereotype-consistent content since Allport and Postman (1945, 1947) found an advantage for race-based stereotype-consistency in their study of rumour transmission. Their study was later replicated in the USA (Treadway & McCloskey, 1989) and similar results found among students in Pakistan (Haque & Sabir, 1975). However, these early studies also demonstrate that, as with the choose-to-receive phase, the extent to which cultural stereotypes are held to be true plays a vital role in whether they are advantaged or not in the encode-and-retrieve phase. Some later research has also found stereotype-consistent information to be more faithfully transmitted than stereotype-inconsistent information in recall-based studies using scientific descriptions of conception (Bangerter, 2000), research reports, and fictional stories (Zhao et al., 2016). Further evidence suggests that stereotype inconsistency may have an advantage in individual recall, but that stereotype consistency bias emerges in recall-based transmission. Kashima (2000) found a recall advantage for stereotype inconsistent content in early generations of a transmission chain, but that overall stereotype consistent content is more faithfully reproduced along entire chains. Similarly, Hunzaker

(2016) found that expectation-inconsistent content is initially more accurately recalled, but content becomes more expectation-consistent through transmission.

MCI bias

Boyer (1994) proposed that humans hold several simple categories ('animal', 'person', 'object' etc) for representations of the world around us, which feature intuitive assumptions about the properties of its members. These intuitive assumptions are referred to as 'folk biology', 'folk physics' and 'folk psychology' and argued to stem from evolved cognitive architecture (Purzycki & Willard, 2016). Concepts which violate category-level assumptions are defined as 'counterintuitive' (Atran & Norenzayan, 2004; Boyer, 1994). This definition distinguishes counterintuitive from unexpected or bizarre, as 'bizarre' concepts might be highly unusual without violating category-level assumptions. Additionally, counterintuitive does not necessarily mean surprising. Counterintuitive concepts are widespread throughout cultures and well understood; a ghost passing through a wall is definitionally counterintuitive but is not surprising to people familiar with ghosts as a cultural concept.

Several studies have found that concepts which are counterintuitive are advantaged in individual memory. An advantage for counterintuitive concepts in short- and longer-term recall has been demonstrated in studies using Native American folk tales and original vignettes in US samples (Barrett & Nyhof, 2001), and in samples from France, Nepal, and Gabon, suggesting a strong, cross-cultural effect of counterintuitive concepts in memory (Boyer & Ramble, 2001). Further studies using lists which varied in the relative proportion of intuitive and counterintuitive concepts found that lists which contain a minority of counterintuitive concepts relative to a majority of intuitive concepts are best recalled, rather than lists of mostly or wholly counterintuitive concepts (Norenzayan, et al., 2006), hence *minimally* counterintuitive bias. An advantage for counterintuitive content has also been found in recall-based transmission using original vignettes (Barrett & Nyhof, 2001), and again was found in cross-cultural samples (Gregory et al., 2019), and biological counterintuitive information has been found to play a more important role in faithful transmission than prestige bias (Berl et al., 2021).

Upal (2007) argues that MCI bias is adaptive as an intelligent agent should evolve to preferentially recall those events or objects which violate the agent's expectations "but can be justified once they have been observed" (Upal et al., 2007, p. 432) and that MCI "concepts of ghosts and gods, when they appear in myths and folk tales, meet these requirements" (p. 433). While an advantage for counterintuitive and MCI content in individual recall and recall-based transmission has been demonstrated, some studies have suggested that this advantage is dependent on the context in which they are presented (Gonce et al., 2006; Upal et al., 2007) and only occurs if their presence contributes to the overall cohesion of the text (Upal., 2011).

Discussion and conclusions

The research reviewed here suggests that several content biases are expressed in the encode-and-retrieve phase of transmission. Emotional arousal is known to play an important role in the encoding and retrieval of memories, but there are mixed results regarding valence and discrete emotions. There is some evidence to suggest a negativity bias in individual recall, but this is subject to significant individual and cross-cultural variation. There is evidence for a threat bias in individual recall and limited evidence for an advantage for threat-related information in recall-based transmission, but this also suggests it is transmitted less faithfully than social information. Similarly, to the choose-to-receive phase, evidence for a stereotype consistency bias in this phase is inconsistent. There is evidence of an advantage for stereotype inconsistent content in individual recall, but stereotype consistent content in recall-based transmission. MCI bias has good evidence in individual recall and recall-based transmission but may rely on context.

Choose-to-transmit

The choose-to-transmit phase of transmission involves an individual choosing information to pass onto another individual or individuals. Content biases in this phase increase the likelihood that content will be selected for onward transmission. This selection may be from information they have retrieved from memory or may involve no recall of

information. While an important element of social transmission, there is a lack research directly addressing the mechanisms of this process within Cultural Evolution research. However, drawing on a socially situated view of human cognition (e.g., Clark, 1998; Smith & Semin, 2007), work within the psychology of communication has emphasised the importance understanding the role of biases in onward social transmission, suggesting that the expression of content biases will be moderated by the context and social goals of that transmission (Fay et al, 2021). This approach provides valuable insights into how the perceived audience (Sedikides, 1990) and motivations of the transmitter (Wade & Clark, 1993) influences the information which is transmitted.

Emotion bias

Research from the psychology of communication has suggested that biases are not invariant but are dependent on the social goals of the transmitter (Fay et al, 2021). The onward transmission of negative content is moderated by the social connection held between transmitter and receiver and a key motivation for the transmitter will be presenting a positive self-image (DiFonzo & Bordia, 2007). Regarding emotional valence in transmission, early research on social transmission from this field demonstrated that people are less likely to transmit bad news, in case it generates negative effect in their conversational partner and creates a negative impression of the transmitter (Rawlins, 1983; Tesser & Rosen, 1975). More recently, Fay et al. (2021) found that negative content was only advantaged in onward transmission in an asocial condition and when the receiver was absent; when the receiver was present (analogous to dyadic conversation), there was no negativity bias in the choose-to-transmit phase of transmission. They argue this is driven by the goal of fostering a positive impression with the conversation partner. While the desire to foster a positive impression may demotivate the transmission of negative information in certain circumstances, this is dependent on the nature of the relationship between transmitter and receiver. In longer-term relationships, utility and authenticity are privileged, and negativity bias is found again (Stevens & Fiske, 1995; Weenig et al., 2001). Support for this audience-based influence on negativity or positivity bias in the choose-to-transmit phase comes from van Leeuwen et al. (2018), who found that people are more likely to choose-to-transmit positively valenced vignettes than negatively valenced equivalents when the audience are strangers, only

preferring to share negative vignettes when the audience are friends. Other research has found that the positive framing of vaccine arguments makes them more likely to be shared, but not more memorable (Altay & Mercier, 2020) suggesting a distinction between motivation to share and recall.

The influence of the relationship between transmitter and receiver on information transmitted also extends to whether they share group membership or not. Individuals are more likely to share a negative rumour about their ingroup with a fellow ingroup member than a positive rumour, and are more likely to share a positive rumour about the outgroup with an outgroup member than a negative rumour (DiFonzo & Bordia, 2007).

Oishi (2002) found that European Americans reported more positive memories compared to East Asian Americans, but this difference was not a result of differences in recall, but a difference in the perceived relevance of positive and negative memories. The European Americans perceived positive content to be more relevant so selected it for reporting, while the East Asian Americans viewed both as equally relevant, reporting both equally. This suggests cross-cultural differences in how positive and negative memories are selected for transmission.

Regarding discrete emotions, descriptions of surprising experiences are more likely to be shared with others (Heath et al, 2001; Hutter & Hoffman, 2014) and more surprising news articles are also more likely to be shared (Berger & Milkman, 2012). However, this association may be driven by arousal rather than a distinct effect of surprise. Eriksson and Coultas (2014) found that more disgusting stories were more likely to be selected to be shared with others than less disgusting stories. This served as a replication of Heath et al. (2001), who also found that the more disgusting a story was, the more people were willing to share it with another person. However, in a second study Eriksson et al. (2016) found that, while a US sample preferred to share more disgusting content, an Indian sample did not, preferring to share stories which evoked happiness and surprise. While Eriksson et al. (2016) argued that cultural differences between samples in response to the disgusting content drove this difference, other studies suggest that audience perception will also impact on the choose-to-transmit phase of transmission. A key limitation of both Eriksson and Coultas (2014) and Eriksson et al. (2016) is that there was no consideration of perceived audience, something which has been shown to influence the onward transmission of emotional material.

Threat bias

Blaine and Boyer (2018) addressed the role of selection in transmission directly by using a transmission chain design which required no recall, instead participants selected items to share with another person. They found that threat-related information was the most likely to be shared, compared to positive, neutral, and negative non-threat-related information. Stubbersfield et al. (2015) found threat-related content to have no advantage over social information in this phase of transmission, although a limitation of this study was that it did not consider the role of audience, which may influence what people choose to transmit. Further, there was no comparison to control material, as such it cannot be concluded whether threat-related information would have an advantage over neutral information or not in this transmission phase. Other research has found threat-related information to be disadvantaged at this phase compared to positively valenced content (van Leeuwen, et al., 2018).

Social bias

There is little research on social bias in the chose-to-transmit phase of transmission. The sole study found that social information had no advantage over threat-related information (Stubbersfield, et al., 2015), but this study did not consider the role of audience, which may influence what people choose to transmit. Further, there was no comparison to control material, as such it cannot be concluded whether social information would have an advantage over neutral information or not in this transmission phase.

Stereotype consistency bias

The apparent discrepancy between individual recall and recall-based transmission for stereotype consistent content (discussed above) was investigated by Lyons and Kashima (2006). Comparing the transmission of stereotype consistent and inconsistent content along cumulative recall chains without communicative intent, and social transmission chains with communicative intent, they only found stereotype consistency in the social transmission

chains. Lyons and Kashima (2006) argue that stereotype consistency bias emerges when people are communicating information to another, as their motivation to be understood increases their use of expectation-based schema. This is consistent with research on ‘cognitive tuning’ which suggests that believing oneself to be a ‘transmitter’ of information influences how information is transmitted, including the rejection of inconsistent information and the altering of content to meet the expectations of the anticipated audience (Guerin & Innes, 1989; Zajonc, 1960). Overall, this suggests that stereotype consistency bias is more a bias of the choose-to-transmit phase than the encode-and-retrieve phase.

Discussion and conclusions

The research reviewed here suggests that several content biases are expressed in the choose-to-transmit phase of transmission, however, there is much greater inconsistency in this phase relative to others. There is mixed evidence for biases for emotional arousal, valence and discrete emotions, with the best evidence being for a bias for disgusting content among Americans. The success of emotional content at this stage appears to be highly dependent on the context of transmission, goals of the transmitter, perceived receivers, and culture. Similarly, the evidence for a threat bias is mixed, and is likely also influenced by transmitter motivations and audience effects (unsurprising given that threat-related information is likely to also have negative valence). There is limited evidence for social information bias. There is evidence for a stereotype consistency bias, but this is also likely dependent on the transmitter’s expectations about their anticipated audience.

Presence in wider culture

Content biases in transmission which have been demonstrated in inter-individual or micro-society experiments (such as transmission chains) should also be supported by evidence from wider culture. We should expect the frequency distributions of cultural traits and artefacts to be shaped by and reflect these content biases. Several studies have examined this across a range of biases. However, natural transmission outside of a laboratory context

cannot be easily separated into choose-to-receive, encode-and-retrieve, and chose-to-transmit phases. Transmission in wider culture may be primarily recall-based, where information is not recorded and so its cultural success is dependent upon encoding in memory, or may be selection-based, where information is recorded and transmitted without the reliance on memory. However, in many instances a combination of all phases will be involved. As such, even with cultural artefacts where recall has played a role, the extent to which recall was involved will vary and is impossible to determine. Other phases will also have played a vital role and in various forms of media (written, visual art, electronic communication) recall would have been absent from some transmission. We can assume that selection plays an important role in authored work (art, journalism etc.) as the author is making a choice to transmit, although in some cases a role for recall cannot be ruled out if memorisation is required for performance (e.g., song lyrics). In electronic communication (which requires no recall), we can be more confident that transmission is primarily selection based. This section reviews evidence for content biases from studies of cultural artefacts.

Emotion bias

It has been long recognised that emotion plays a role in the selection of stories to feature on the front page of newspapers (e.g., Danson & Soothill, 1996; Sorenson et al., 1998). With the onset of social media and the ability of individuals to share content via electronic means, the sharing of content, particularly news, online has drawn interest from researchers in communication and media (see Kümpel et al., 2015 for systematic review of research on sharing of news content on social media). Some research suggests a general advantage for more emotionally arousing content online (Brady et al., 2017; Stieglitz & Dang-Xuan, 2013; but see critiques in Burton et al., 2021). Other research suggests an advantage for negative content, finding evidence for negativity in online “fake news” articles (Acerbi, 2019), within online “echo chambers” (Asatani et al., 2021; Del Vicario et al., 2016), in tweets about political events (Bellovary et al., 2021; de León & Trilling, 2021; Schöne et al., 2021), in tweets about electoral conspiracy theories (Youngblood, et al., 2021) and in tweets about a climate change summit (Hansen, et al., 2011). However, this is not universal, other research has found evidence for positivity bias in the sharing of news content on social media (Bakshy et al., 2011; Trilling et al., 2017). Although this varies between

platforms, with the effect being more pronounced on Facebook than Twitter (Trilling et al., 2017). Considering both negative and positive content, research has found that while negative sentiment might increase the speed of retweeting, tweets with positive sentiment received more retweets overall and reached more people (Ferrara & Yang, 2015). The relative advantage of positive and negative content online may depend on domain, with some domains, such as climate change advantaging negative content, and others, such as same-sex marriage, advantaging positive content (Brady et al., 2017). In a content analysis of 260 randomly selected urban legends (a form of contemporary folklore with a tradition of oral, typically recall-based transmission, but also involving other forms of transmission without recall), Stubbersfield et al. (2017b) found that the most frequently evoked emotion was a positive one: amusement; and that anger was the least commonly evoked emotion.

In studies of recorded artistic work, both the lyrics (Brand et al., 2019) and the emotional music cues (Schellenberg & von Scheve, 2012) of popular music have increased in negative sentiment over the last fifty years, and more negative songs do better in the charts (Brand, et al., 2019). The use of positively valenced emotion words has declined relative to a near stability of negatively valenced emotion words in Anglophone literature since the start of the 18th century (Morin & Acerbi, 2017).

The valance of emotion is not the only aspect to generate variation in the sharing of cultural artefacts. Research suggests that arousal increases the likelihood of sharing news content (Berger & Milkman, 2012), even if that arousal is incidental to the content being shared (Berger, 2011). Further, news content is more likely to be shared if it evokes high arousal, ‘activating’ emotions (such as awe, anger and anxiety) than low arousal, ‘deactivating’ emotions (such as sadness) (Berger & Milkman, 2010, 2012). However, recent research found that content evoking sadness can be shared more than content evoking anger, suggesting that the role of activation in sharing behaviour may need to be reevaluated (de León & Trilling, 2021). This may in part be driven by audience effects, as sharing a political article evoking sadness may be less controversial and less likely to inspire conflict with others in their social network (de León & Trilling, 2021). In a study explicitly examining the attention paid (choose-to-receive) to and the sharing (choose-to-transmit) of news content online, Ørman (2019) found that the emotional sentiment of content was a poor predictor of attention and sharing behaviour relative to other factors.

Regarding, discrete emotions, evidence for an advantage for surprise can be found in the wide cultural success of the repetition-break narrative structure. In the repetition-break structure, repetition of similar events creates a trend, which is then ‘broken’ by a contrasting event which generates surprise, for example in the folktale Three Little Pigs (Aarne-Thompson-Uther type 124, Aarne & Thompson, 1961), the trend of the Wolf’s success in blowing down their houses is broken by his failure with the final house (Loewenstein & Heath, 2009). The repetition break structure has been found in large numbers of jokes, Western art music, and jazz music (Rozin et al., 2006) and in a sample of international folktales (Loewenstein & Heath, 2009). Further, advertisements which use the repetition-break structure receive more views on YouTube and are more likely to win awards (Loewenstein, 2011).

Threat bias

Orally transmitted, and therefore typically recall-based, folklore across cultures provides examples of narratives which contain ecological information relevant to survival (Sugiyama, 2001). Information relevant to hunting game, gathering edible plants and avoiding dangerous carnivores can be found in the oral narratives of the Ju/’hoansi (Biesele, 1993), !Kung (Biesele, 1978), White Mountain Apache (Goodwin, 1939) and Yanomamö (Wilbert & Simoneau, 1990), while information related to threats and harmful events are common in Western rumours (Knapp, 1944) and urban legends (Stubbersfield et al., 2017).

Davis and McLeod (2003) examined the front pages of an international selection of newspapers spanning 1700 to 2001 and found that threat-related content, stories about accidental death, or murder, were the most commonly featured themes, and that this was relatively stable over the three-hundred years. They argued that this was a result of evolved preferences driving story selection. In a content analysis of online ‘fake news’ articles, Acerbi (2019) found that threat-related information was present, especially when related to politics, but to a lesser extent than social information and information about celebrities.

Social bias

While there has been little direct examination of social bias in cultural evolution outside of the laboratory, researchers have argued that successful narratives often involve the dilemmas of social relationships (Mar & Oatley, 2008) and traditional folktales across cultures often concern social topics such as kinship, marriage, sex, friendship, betrayal, social status, interpersonal conflict, and deception (Sugiyama, 2001). In the same content analysis of urban legends mentioned previously, Stubbersfield et al. (2017b) found that a significant majority contained social information. The prominence of public personalities and celebrities (i.e., social information) has been found to play an important role in the sharing of genuine news content (Ørman, 2019) and in online ‘fake news’, alongside other aspects of social information (Acerbi, 2019). In their study of international newspaper front pages, Davis and McLeod (2003) found that social-related themes, such as reputation, altruism, and marital courtship, were very common across the three-hundred years. In an analysis of posts and interactions on the French Facebook page Santé + Mag, a page known as a source of online health misinformation (i.e., threat related content), over 50% of posts contained social information and only 27.8% contained threat-related information, with post interactions primarily serving a social function (Berriche & Altay, 2020).

MCI bias

The presence of MCI and counterintuitive content in recall-based cultural evolution has been relatively well examined, although almost entirely focused on traditional folktales (to a large extent the concept of MCI bias was developed through research on these tales). Culturally successful Grimm’s Brothers’ folktales have been found to fit the MCI template (i.e., contain a small number of counterintuitive concepts relative to a majority of intuitive concepts), with a ‘cognitive optimum’ of two to three counterintuitive concepts proposed (Norenzayan et al., 2006). Other optimums have been suggested, however. Based on an examination of a global sample of folktales Barrett et al. (2009) suggested a cognitive optimum of one or two counterintuitive concepts. Outside of traditional folktales, a study of counterintuitive concepts in Ancient Roman Prodigia (stories about portentous events

signalling divine displeasure) by Lisdorf (2004) found evidence of MCI bias in line with the cognitive optimum proposed by Barrett et al. (Barrett, 2008; Barrett et al., 2009). For more contemporary examples, analysis of variations of the 'Bloody Mary' urban legend (which typically describes the supernatural summoning of a ghost) (Stubbersfield & Tehrani, 2013) and descriptions of over 19,000 American comic book characters (Carney & Carron, 2017) found that variations were typically in line with the optimum suggested by Norenzayan et al. (2006).

A broader analysis of urban legends found MCI content to be rare relative to other bias-evoking content, but in line with the Barrett et al. optimum (Barrett, 2008; Barrett et al., 2009) when present (Stubbersfield, et al., 2017b). Similarly, Acerbi (2019) found that MCI content was present in online 'fake news' but to much less a degree than content evoking other biases. It should be noted that some of the experimental work discussed above (e.g., Gonce et al., 2006; Upal., 2011; Upal et al., 2007) opposes the 'cognitive optimum' concept, emphasising that MCI bias only functions if the counterintuitive concepts are part of a coherent story (a point also supported by the analysis of Bloody Mary legends by Stubbersfield and Tehrani, 2013).

Discussion and conclusions

The research reviewed here suggests that there is evidence for several content biases in examinations of wider culture. More emotive content appears to be more culturally successful, with some evidence for negativity bias and surprising content, but there is some inconsistency regarding valence, and discrete emotions, with the context of transmission likely playing an important role. There is evidence for threat bias cross culturally, but it appears to be less prominent than social bias, especially in contemporary Western cultures. MCI bias is represented in the content of traditional, cross-cultural folktales but seemingly less so in contemporary narratives such as urban legends and fake news. There also remains a debate about a 'cognitive optimum' for counterintuitive concepts.

General discussion and conclusions

While research within cultural evolution often focuses on the role of context biases in transmission, recent research suggests that content biases are as influential, or more influential than context biases on the selection (Acerbi & Tehrani, 2018), faithful transmission (Berl et al., 2021) and wider dissemination of information (Youngblood, et al., 2021). Here research examining content biases is reviewed, with a focus on considering these biases across three phases of transmission: choose-to-receive, encode-and-retrieve, and choose-to-transmit. Through reviewing literature from cultural evolution and relevant literature from the psychology of attention, memory and communication, it is clear that several content biases are well demonstrated, with evidence from laboratory studies and studies using observational data supporting their role in cultural transmission in the three phases. There is particularly strong evidence for an emotional bias for arousing content across all three phases, however, while there is some support for a general negativity bias across all three phases, evidence is inconsistent, suggesting an important role of context and individual and cultural variation in emotion bias. For other biases there is relatively consistent support in the choose-to-receive and encode-and-retrieve phases but more inconsistent evidence in the choose-to-transmit phases, where the context of transmission and expected audience appear to play an important role. Further, there is inconsistency in evidence and approach which makes it difficult to directly compare the evidence base of the different biases. This review highlights two key points:

1. There is a need for greater engagement between cultural evolution researchers and relevant research from other fields.
2. There is a need for a more consistent approach to studying content biases with focus on the processes involved in their operation.

Point 1 is challenging as there is a wealth of research relevant to content biases in cultural evolution from the fields of attention, memory, the psychology of communication and related areas of interest (e.g., rumour psychology). When considering three phases of transmission, research from these fields is directly relevant to what content people chose-to-receive, what content they will successfully encoded-and-retrieve, and what content they will chose-to-transmit to others. Further, evidence from these fields suggests significant individual and cultural variation across the phases, which is not often considered within cultural

evolution approaches to content biases. While key results have been summarised, the wealth of research in these fields is beyond a detailed review here, as such relevant reviews of literature within these fields have been cited. As a full understanding of multiple, diverse research fields with extensive histories is largely beyond the abilities of individual researchers, this stands as a call for further collaboration and engagement with fields beyond cultural evolution. These fields can contribute to our understanding of how biases may function in transmission across the three phases, while cultural evolution theory can provide a valuable framework to understand how these biases result in population level patterns, moving beyond the individual and inter-individual focus of many of these fields and contributing novel methods and approaches to research.

For point 2, I recommend a more consistent approach to examining content biases experimentally. My first recommendation is to consider the three phases separately, to enhance our understanding of the mechanisms involved in each individual bias, and how biases might differ (or not) across these phases. While this approach was initially proposed by Eriksson and Coultas (2014), very few studies have taken a similar approach since. A second, related recommendation is for greater understanding and clarity about the role of communicative intent in linear transmission chains. Some linear transmission chain experiments involve no expectation by the participant that what the recall will be passed on to another participant (essentially studying cumulative recall), while in other studies participants are aware that what they recall will be passed on, and therefore the nature of transmission may be influenced by communicative intent. Communicative intent has been demonstrated to influence the presence of content biases are found in transmission chains (see Lyons & Kashima 2006, and to a lesser extent Stubbersfield, et al., 2019), so it is important to engage with this and preferably test using both types of chain. Further, transmission chains have long been criticised for omitting essential properties of interpersonal interactions and communication processes (see DiFonzo et al., 1998; Pelletier & Drozda-Seknowska, 2020; Rosnow, 1980). For example, they have been criticised for the lack interaction between transmitter and receiver, interaction which would likely influence the nature of information transmitted (Middleton & Edwards, 1990). While transmission chains will remain valuable for examining the processes and mechanisms of interpersonal cultural transmission it is important to consider how the interactive, dynamic nature of communication influences the expression of these biases. Future experimental approaches should draw influence from developments in the psychology of communication which emphasise the importance of social

context and relationship between transmitter and receiver (see Fiedler, 2007; Pelletier & Drozda-Senkowska, 2020).

A key reason to take the three phases approach is that some biases may operate differently across the phases. This is demonstrated in Lyons & Kashima (2006) where stereotype consistency bias appears only as a bias of onward transmission with communicative intent, not, seemingly, of individual attention (choose-to-receive) or memory (encode-and-retrieve). This is supported more broadly in the literature on the transmission of stereotype content, with expectation breaching stereotype inconsistent content being favoured in attention and recall (Kashima, 2000) and stereotype consistent information being favoured by social communication and transmission (Lyons & Kashima, 2006). From reviewing the current evidence, it is plausible to hypothesise that some content biases primarily function as biases of attention and memory, while others primarily function as biases of onward transmission. For example, the strongest evidence for threat bias and negative emotion bias comes from studies of the choose-to-receive and encode-and-retrieve phases, while evidence from the choose-to-transmit phase is less consistent or suggests no advantage for these types of content, suggesting they primarily function as biases of attention and memory. For other biases, such as stereotype consistency bias and positive emotion bias, the most consistent evidence comes from the choose-to-transmit phase or suggests an important role of communicative intent, suggesting they primarily function as biases of onward transmission. Relatedly, recent research has found that biases for negative emotion, disgust, and threat-related content are stronger in recall-based transmission, than selection-based, although negative content did have an advantage over neutral content in both modalities (Acerbi, 2022).

This potential distinction is consistent with the suggested origins of these biases. We would expect biases which evolved to provide a fitness advantage (as has been suggested of threat related and negative emotion biases) to be primarily present in our attention and memory, while biases which function to promote social affiliation or serve communication (suggested of positive emotional and stereotype consistency biases) would be expected to primarily present in our sharing of information with others. This difference is intuitive; a disgusting urban legend might draw our attention and stay in our memory, but we are unlikely to pass it on indiscriminately, our choice to share it will be influenced by a range of contextual factors. It is already understood that the sharing of news, and 'fake news', is driven by concerns about our reputation and social status (Altay et al., 2019; Bright, 2016):

we might enjoy reading sensationalist stories high in content which evokes negative emotions in private, but in a public or semi-public arena, we want to be seen to be sharing content which serves to enhance our reputation (Ørman 2019). This distinction also helps us understand the inconsistencies between phases, a negativity bias in impression formation (choose-to-receive phase) is congruent with a positivity bias in communication to potential affiliates (choose-to-transmit phase), as we are seeking to avoid fostering a negative impression.

That content biases may function differently across the three phases, especially between memory, and selection to share, has implications for wider cultural evolution. This is especially the case with the onset of electronic communication, which allows for the easy transmission of information based purely on selection, without any need to encode that information and retrieve it from memory. Content biases operating on the choose-to-transmit would be advantaged by electronic modes of communication, while content biases operating on the encode-and-retrieve phase would not. This is already visible to some extent in the transmission of emotive content online, with research suggesting an advantage for positive emotional content in social media sharing (Bakshy et al., 2011; Ferrera & Yang, 2015; Trilling et al., 2017). However, it should be noted that some biases which may primarily function as memory biases, such as threat bias, have been found to be present in both recall-based and electronic-based cultural evolution (see Stubbersfield et al., 2017b and Acerbi, 2019 respectively). The extent to which this difference in phase operation leads to differences in population patterns is an empirical question, but one warranting research. Agent based models could be used to assess if biases at different phases produce differences in the frequency distribution of traits at the population level.

Further, consideration of how biases may operate differently within the distinct phases could help identify whether cultural change is being driven by cultural selection or biased (or convergent) transformation dynamics (see Acerbi et al., 2021; Mesoudi, 2021). As recall can be a reconstructive process, biases in the encode-and-retrieve phase may produce biased transformation in cultural transmission, as seen in the negative transformation of ambiguous events in a transmission chain (Bebbington, et al., 2017). Biases operating primarily in the choose-to-receive and choose-to-transmit phases, however, should produce cultural selection dynamics, especially if recall is absent from the process. However, as biased retellings of information can influence the memory of that information (Tversky & Marsh, 2000), biases

in the choose-to-transmit phase may transform what is encoded. As such, interactions between the phases and their role in transformation and selection should also be considered.

Currently, there is too little consistency and coherence in approach to testing content biases to clearly conclude that some operate primarily as attention and recall biases and others primarily function as selection and onward transmission biases. The disparity in evidence across different phases is largely a product of research focus rather than consistent comparison. For example, the evidence for threat bias is strongest in the encode-and-retrieve phase relative to other phases, but this is primarily because of a research focus on individual memory and a scarcity of research focusing on other phases. As such, any differences remain hypothetical. It would also be beneficial to consider content beyond text (as in Schellenberg & von Scheve, 2012), as there is currently an over-reliance on text-based studies, and to consider the relative strength and interaction of content biases (as in Berl et al., 2021; Stubbersfield et al., 2015), and the relative strength and interaction between content and context biases (as in Berl et al., 2021), as types of content will rarely appear in isolation. Further, cross-cultural research in cognitive science suggests that cognitive capacities are influenced by culture resulting in cross-cultural differences in perception, attention, memory, and social cognition (see Barrett, 2020; Henrich et al., 2010), all of which could impact on the expression of content biases in the three phases across cultures. Most of the cross-cultural evidence for transmission biases has focused on context biases (e.g., prestige bias in Henrich & Broesch, 2011), and while there have been some cross-cultural studies of content biases, the majority have been reliant on data collected from Western, educated, industrialised, rich, and democratic (WEIRD, see Henrich et al., 2010) populations.

To conclude, research from a range of fields and using a variety of methods supports the existence of a number of content biases in cultural transmission. There is some suggestion that these biases may operate differently across three phases of transmission (choose-to-remember, encode-and-retrieve, choose-to-transmit), with the potential that some biases primarily function as biases of attention and memory, while others primarily function as transmitter biases with implications for wider cultural evolution, however, a more consistent approach to research and greater engagement with literature from other fields is required to fully understand how content biases operate.

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