Box 1. Outstanding questions

- To what extent is the auditory awareness-related negativity related to the visual awareness negativity (see 'EN' effects in Figure 1), and can either of these be isolated from attention-related activity (or other precursors of consciousness)?
- What portions of auditory cortex are activated differentially depending on awareness of stimulus presence/absence, awareness of specific perceptual details, and awareness of changes in perceptual content?
- What is the role of late activity in frontal and parietal circuits (indexed by late positive responses) in auditory and visual awareness, and are the same frontal and parietal regions activated across the two modalities?
- To what extent do auditory and visual cortices interact before, during, and after conscious perception of objects when auditory and visual information about an object arrive simultaneously?
- Are individual differences in conscious perception stable across sensory modalities – for example, the severity of changeblindness/deafness, susceptibility to inattentional blindness/deafness, switching-rates for bistable stimuli, or perceptual thresholds for masking?
- In what situations are auditory NCCs more useful than visual NCCs for assessing the integrity of consciousness in clinical populations with disorders of consciousness, and in what ways can auditory NCCs be used to enable communication with people suffering from severe brain damage?

Concluding remarks

Extending work on visual NCCs into the auditory domain shows potential to offer unique insight from both a methodological and theoretical perspective. As experimental paradigms continue to be refined, future studies should attempt to carefully control for attention and task-related confounds, and consider testing the same participants on closely matched auditory and visual tasks to allow more direct comparisons of NCCs across sensory modalities.

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Emotional contagion: its scope and limits

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The contagion model of emotional propagation has almost become a dogma in cognitive science. We turn here to the evolutionary approach to communicative interactions to probe the limits of the contagion model.

The appeal of the contagion model

According to much recent work in cognitive social neuroscience, the propagation of emotions between individuals is essentially a replicative process variously termed

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'contagion', 'resonance', 'sharing', 'mirroring', and 'direct matching' [1]. The currently prevalent contagion model of emotional propagation is a two-step model: first, the perception of another's expressive behavior automatically causes the observer to covertly replicate the agent's behavior. Second, the covert replication of the agent's behavior automatically causes the observer to share the agent's affective or emotional state [1,2]. Interestingly, one may trace the early emergence of this contagion model to Gustave Le Bon's epidemiological approach to crowd psychology [3] (Box 1).

What makes this parsimonious model appealing is that it offers the prospect of a unified account of human social cognition along the following lines. When an agent performs a goal-directed instrumental action, her intention can be construed as the cause of her bodily movements.



Forum

Box 1. Emotions as 'infectious diseases': a long intellectual history

One early precursor of the contagion model of emotional propagation is the investigation of crowd psychology by Gustave Le Bon in his 1896 book, The Psychology of Crowds [3]. Le Bon's seminal focus on crowd behavior was in part motivated by the fears of members of the French political and intellectual establishment who perceived crowd behavior as a threat to the stability of the social order. Le Bon advocated an epidemiological approach to emotional contagion: he explicitly linked the propagation of emotions to the spread of germs. Although emotional contagion is often construed as a major source of social understanding [1,2], Le Bon highlighted instead the deleterious effects of emotional contagion: he argued that crowd behavior deprives crowd members of their ability to act rationally. However, contrary to the traditional expectation that contagious fear inevitably turns into crowd panic, which is likely to threaten the persistence of social norms, recent careful examination of real emergency situations (e.g., September 11th, 2001) shows that cooperation is preserved and can even be fostered in large groups of people in the presence of threatening events [10].

Similarly, an agent's emotion can be construed as the cause of her expressive behavior. The two-step model affords an elegant account of human social responses to the perception of both another's goal-directed action and another's expressive action: in the former case, the observer is taken to automatically share (or resonate with) the agent's goal or intention. Moreover, the model can even integrate findings from the neuroscientific investigation of the responses of both human and non-human primates to the perception of the goal-directed actions of others. In the case of expressive actions, the observer is taken to automatically share (or resonate with) the agent's emotion or affective state [2].

Is emotional propagation always replicative?

Although elegant, the contagion model is questionable on both empirical and theoretical grounds. First, the uncritical acceptance of the contagion model in the investigation of some core social cognitive processes, for example pain, has to some extent obliterated the boundaries between four distinct phenomena: feeling physical pain, empathizing with another's pain, contagious pain, and sympathetic responses to another's pain [4].

Second, the contagion model rests on the assumption that emotional propagation is a replicative process: the default response to the perception of another's emotional display should always be to experience the same emotion as the agent. However, emotional similarity is unlikely to be the default response to the perception of all emotional displays between every pair of individuals. Although the perception of another's expression of fear or disgust may cause another to feel fear or disgust, the perception of another's display of anger is likely to trigger fear and submission, not anger [5]. Plainly, the perception of cues of another's embarrassment, envy, or jealousy about a third party does not automatically elicit a similar feeling of embarrassment, envy or jealousy. Nor does the perception of cues of another's pride, pain, or sadness. It all depends on which emotional display is involved, on the agent's identity, the recipient's identity, and the nature of their interaction, for example whether they are in- or out-group members, and whether they are cooperating or competing [6].

Much of the current appeal of the contagion model rests on the similarities between goal-directed actions and expressive actions. But, there are obvious dissimilarities: a goal-directed instrumental action is an efficient means selected by an agent to fulfill her desire in light of her beliefs. However, it is unclear whether emotional displays can be construed as efficient means at all. Only if emotional displays have a function can they be construed as efficient means. The basic question therefore is: what is the function of emotional displays?

What is the function of emotional displays?

One way to address this question is to construe emotional displays as constituents of what evolutionary biologists term communicative interactions. A genuine communicative interaction is a change caused by an agent to a recipient whereby the former sends a signal to which the latter responds. This in turn is the case only if both the agent's action and the recipient's response have been shaped by natural selection. If only the agent's display or the recipient's response has been shaped by natural selection, then either the interaction is coercive or the agent has produced a mere cue. According to this evolutionary framework, emotional signals have co-evolved with recipients' behavioral responses [7].

Moreover, evolutionary biologists draw a distinction between ultimate and proximate explanations. Ultimate explanations of a behavioral trait deal with its fitness benefit and seek to answer why-questions by shedding light on the biological functions of the trait – why do emotions propagate at all across individuals? Proximate explanations seek to answer how-questions and to shed light on how the function of a trait is achieved: how do emotions propagate? What particular psychological mechanism underlies emotional propagation? Thus, a satisfactory explanation of a behavioral trait (e.g., emotional propagation) depends on the interplay between proximate and ultimate explanations [7].

The coordination between the sender and the recipient of an emotional signal will be evolutionarily stable only if producing the signal and responding to it are advantageous to both the sender and the receiver [7,8]. Producing a display makes the agent vulnerable to a predator, and the recipient is vulnerable to the sender's deception. If the conditions for the stability of emotional communication are met, then emotional parity (or replication) is likely to emerge in some, but not in all, cases: one and the same emotional state (such as fear) may cause one and the same adaptive behavioral response (such as flight) in both the sender and the receiver. However, if the sender expresses anger, pride, or sadness, then the recipient is more likely to produce a contingent, in other words a complementary, response than to replicate the sender's display.

Concluding remarks

The contagion model offers a proximate mechanism in answer to the question: how do human emotions propagate? The proximate mechanism favored by the contagion

Box 2. Ostensive emotional communication

As the study of pragmatics has shown, much of human communication is ostensive. An act of communication is ostensive when the communicative agent does not merely intend to convey some information (for example, about danger) to her recipient, but also intends the recipient to recognize that she has the above informative intention [11]. Some evidence shows that preverbal infants are uniquely sensitive to caretakers' ostensive signals (e.g., direct gaze, motherese; i.e., the spontaneous adaptation of adult speech for addressing young infants, Figure I) [9]. An important question for further research is whether emotional displays can also be part of ostensive communicative acts. Some evidence suggests that young children learn to regulate their emotions from observing their caretakers ostensively mirror their own emotional displays of emotion such as fear or sadness [12]. Despite the fact that the caretakers' behavior replicates that of the child, the latter must be able to interpret their caretakers' behavior as a contingent response to, not a mere copy of, their own emotional display.



Figure I. After seeing an agent gaze at one of two objects, children aged 6 months followed the agent's gaze only if the agent had antecedently produced one or the other of two ostensive signals: eye-contact or speaking in motherese. Figure from [9], courtesy of G. Csibra and G. Gergely.

model is emotional replication. We have argued that emotional propagation is unlikely to be replicative in all cases. Moreover, emotions could not propagate unless one agent produces an emotional display which a recipient can perceive and respond to. Producing an emotional display, and attending and responding to it, are costly activities. The fundamental question is: what is the biological function of emotional displays? As we have further argued, much light can be shed on this question by construing emotional displays as signals conveyed by a sender to a receiver subject to the constraint that the benefits of the communicative interaction are greater than the costs for both the sender and the receiver.

For the purpose of further testing this communicative approach to emotional propagation, one direction for future experimental research would be to investigate the extent to which the sender of an emotional signal spontaneously takes into account the epistemic needs of her recipient. For example, it would be worth testing whether a sender would spontaneously modulate the intensity of her facial or bodily emotional display to accommodate known changes in her recipient's epistemic access to the information conveyed by her signal, as a function of the amount of surrounding noise. A further related question for future research is whether human caretakers or teachers can turn emotional displays into pedagogical cues for the purpose of deliberately conveying novel information to children or students (Box 2) [8,9].

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