Audiovisual perception

Implicit estimation of sound-arrival time

In perceiving the sound produced by the movement of a visible object, the brain coordinates the auditory and visual input[1–3] so that no delay is noticed even though the sound arrives later (for distant source objects, such as aircraft or firework displays, this is less effective). Here we show that coordination occurs because the brain uses information about distance that is supplied by the visual system to calibrate simultaneity. Our findings indicate that auditory and visual inputs are coordinated not because the brain has a wide temporal window for auditory integration, as was previously thought, but because the brain actively changes the temporal location of the window depending on the distance of the visible sound source.

Seven subjects with normal vision and hearing were presented through headphones with a burst of white noise (90 decibels sound-pressure level, 10-ms duration, with 4-ms rise and fall times), the spectrum of which had been processed (by using head-related transfer functions) to simulate an external sound from a frontal direction. Brief light flashes (10 ms) were produced by an array of five green light-emitting diodes (LEDs) at different distances from the subjects (1–50 m; Fig. 1). The intensity of the light flash was 14.5 candelas per square metre at a viewing distance of 1 m, and was increased in proportion to the square of the viewing distance for the other distances in order to produce consistent intensity at the eye. The difference in onset times between the sound and light stimuli was varied randomly from −125 ms to 175 ms in steps of 25 ms.

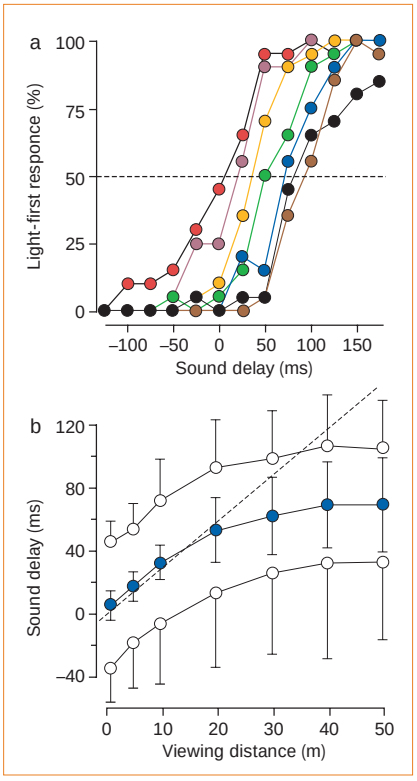

Figure 1 Synchrony in audiovisual perception. **a,** Representative results from one observer. The percentage of light-first response for each viewing distance is plotted against sound delay (stimulus-onset asynchrony). Different colours represent results for different viewing distances (red, pink, yellow, green, blue, brown and black correspond to 1, 5, 10, 20, 30, 40 and 50 m, respectively). Dashed line indicates the 50% point, which corresponds to subjective simultaneity. **b,** Points of subjective equality (filled circles) plotted against viewing distance. Hollow circles, plots of 25% (bottom curve) and 75% (top) of light-first response indicate the threshold for detecting asynchrony. Dashed line represents the real sound-arrival time.

Subjects were instructed to look at the centre of the LED array and to imagine that the LEDs were the source of both light and sound, while listening to the sound directly from the sound source. To eliminate possible bias effects, we used a two-alternative forced-choice task to measure subjective simultaneity: in this task, observers judged whether the light was presented before or after the sound. Twenty responses were obtained for each condition. To determine the stimulus-onset asynchrony that corresponded to subjective simultaneity, we estimated the 50% point (the point of subjective equality) by fitting a cumulative normal-distribution function to each individual's data using a maximum-likelihood curve-fitting technique.

When the LED array was 1 m away, the point of subjective equality occurred at a sound delay of about 5 ms; however, the sound delay at this point increased with viewing distance ($P < 0.001$; Fig. 1a, b). This increased delay was roughly consistent with the velocity of sound (about 1 m per 3 ms at sea level and room temperature), so the point of subjective equality increased by about 3 ms with each 1-m increase in distance. This relationship was consistent at least up to a distance of 10 m.

Our results show that the brain probably takes sound velocity into account when judging simultaneity. However, it takes about 120 ms for sound to travel 40 m, and we found that the threshold for detecting the sound delay was 106 ms at a viewing distance of 40 m, so active compensation is likely to operate only for shorter distances than this.

We have shown that the brain takes sound velocity into account when integrating audiovisual information. The brain can therefore integrate audiovisual information over a wide range of temporal gaps, and correctly match sound and visual sources.

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Competing financial interests: declared none.

COMMUNICATIONS ARISING

Sociology

The puzzle of human cooperation

Humans often defy rational-choice theory by cooperating in simple dilemma games[1], a paradox that has been explained by theories of kin selection[2], reciprocal altruism[3] and indirect reciprocity (reputation)[4]. Fehr and Gächter claim that human cooperation remains an evolutionary puzzle because people will cooperate with genetically unrelated strangers, often in large groups, with people whom they may not meet again, and without any gain in reputation ('strong reciprocity')[5] — that is, when existing theories do not seem to apply. However, we argue that those theories are rejected for the wrong reasons and that the paradox may therefore be imaginary. This has implications for whether punishment is crucial to promoting cooperation[5–8].

First, strong reciprocity is not necessarily a puzzle because altruistic tendencies need not reflect contemporary selective pressures. Rather, they may reflect motivations that evolved during the past 5–7 million years, in situations that were very different from those presupposed in the puzzle (small groups with relatedness greater than random, individuals well known to each other, interactions likely to be repeated, and people organized in hierarchies). The puzzle disappears if human brains apply ancient tendencies to cooperate that persist in newer environments, even if they are maladaptive (heuristic rules that violate expected utility often make sense for common tasks in our evolutionary history).

Accordingly, kin selection, reciprocal altruism and indirect reciprocity need not explain why altruism fails to conform to rationality theory today; rather, they explain why it became ingrained in our brains in the past. Today, humans distinguish and favour kin, or select partners with whom to repeat games, but this does not conflict with those explanations (it supports their legacy in our evolution). The cost of errors may be high but they are recent, so it is unclear whether selection has been strong (or fast) enough to realign humans' strategic behaviour specifically to deal with modern problems — evidence for systematic deviation from rational solutions indicates that it has not. Such deviations occur across cultures[1], suggesting an ancient and/or common

origin, rather than a fine-tuning to varied modern circumstances.

Second, the punishers in laboratory experiments such as Fehr and Gächter's are anonymous[5], so potential extra costs resulting from retaliation (of any sort) by victims are ruled out. Anonymity is unrealistic among early human groups: vigilantes would have to confront defectors to punish them, which incurs risk, and punishment among group members gives rise to grudges and reprisals, which undermine future cooperation. Although groups may be willing to punish individual defectors, people in one-on-one situations may not accept the personal cost of punishment (for example, they are often unwilling to intervene in criminal acts or to testify in trials for fear of retaliation).

Third, the problem remains of what prevents the occurrence of second-order free-riders, who cooperate for the public good but defect from bearing the cost of punishment[9]. Fehr and Gächter's results suggest that this is not a problem, as a core of people willingly incur personal costs to administer punishment, motivated by anger (although it is unclear whether they would act on it if they were not anonymous).

Alternative solutions are that punishment may come from an external institution, or it is not costly, or is administered to both defectors and individuals who fail to punish defectors. These alternatives have been criticized[9] but, if punishment is important, we suggest that an important source has been overlooked. The 'external' solution has been rejected because cooperation is prevalent in pre-industrial human groups, despite the absence of the enforcing institutions of modern states[9] — but this ignores religion, a feature of all human societies. Religions share taboos and codes of conduct that often promote cooperation for the public good and threaten supernatural punishment for those who do not follow these codes. Followers fear the personal consequences of defecting, and may be prepared to be altruistic if they believe that those who are not will be punished (now or in an afterlife).

A belief in supernatural punishment may arise as an abstract product of culture but thereafter become subject to selection (that is, the argument does not rely on invoking evolutionary origins for religious beliefs). But such beliefs could have evolved, either by group selection[8] or natural selection — as with the 'green beard' effect, individuals who signal common attributes can cooperate selectively with each other and thus outperform others. Groups with costly religious beliefs that signal commitment and loyalty outlive non-religious groups as a result of improved cooperation[10]. A 'stick' may be a good way to coerce people into cooperating, but the 'carrots' of kin cooperation, reciprocal altruism, reputation-building and religion have been crucial alternatives over our long evolutionary history, with a legacy that pervades today.

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Fehr and Gächter reply — The claim by Johnson *et al.* that human cooperation in social-dilemma games violates rational-choice theory is not justified[1]. If people have altruistic aims, altruistic behaviour is a rational means by which to achieve their proximate goals. From an evolutionary viewpoint, we need to explain why humans are often altruistic by strong reciprocity[2–4]. Although kin selection, reciprocal altruism and indirect reciprocity explain relevant forms of human cooperation[5–7], they do not ultimately explain strong reciprocity[8].

Kin selection would account for strong reciprocity if human behaviour were driven by rules that do not distinguish between kin and non-kin. But humans, like other primates, distinguish cognitively and behaviourally between the two[5,9], and generally feel stronger emotions towards kin. Likewise, reciprocal altruism could account for strong reciprocity if humans' behavioural rules did not depend on the probability of future interactions with potential opponents. But humans can distinguish long-term partners from people with whom future interaction will be less likely ('strangers'), and will cooperate more if they anticipate that interaction will be frequent[6]. Emotional responses may also be stronger towards a long-term partner than towards a 'stranger' (our unpublished results).

Reputation-based ultimate theories could account for strong reciprocity if our behavioural rules did not depend on our actions being observed by others. However, if reputation formation is ruled out, cooperation breaks down, whereas it flourishes if subjects gain in reputation[7].

Early humans whose behaviour was fine-tuned to respond to kin or non-kin, partners or strangers, and gaining in reputation, probably had an evolutionary advantage because, contrary to common belief, they faced interactions where the probability of future encounters was sufficiently low as to make defection worthwhile. Ethnographic evidence indicates that humans had many encounters with individuals with whom they had little future interaction[8]. In addition, the costs of mistakenly treating unrelated individuals as kin, or treating strangers as partners, were high — for instance, a lack of vigilance with strangers could be fatal. Because of these costs, individuals who could adjust their behaviour to suit the their opponent's characteristics had greater fitness. The problem with any theory claiming that strong reciprocity is maladaptive in modern circumstances is that individuals understand the risks of exploitation in interactions with non-kin and strangers, and behave accordingly. An evolutionary explanation of strong reciprocity is needed that does not assume that individuals are maladapted[2,3].

A proximate mechanism of belief in supernatural punishment does not solve the evolutionary puzzle. How could such beliefs evolve if those who did not hold them defected and hence gained an advantage? Laboratory experiments do not support the claim that religion is important for cooperation. If other people in the group are expected to defect, then almost everyone else — religious or not — will defect too[10]. Moreover, in almost all religions, non-believers have been ostracized and have faced worldly punishment.

We do not agree that anonymity is a problem in the experiment: it rules out other, less costly forms of social punishment that are available in non-anonymous situations, such as workers' hostility towards strike-breakers and people's hostility towards wartime deserters. If non-anonymous punishment were lessened by being more costly, this could be just another example of how remarkable humans are at fine-tuning their behaviour to suit their circumstances.

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