Perceptual causality and animacy

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Certain simple visual displays consisting of moving 2-D geometric shapes can give rise to percepts with high-level properties such as causality and animacy. This article reviews recent research on such phenomena, which began with the classic work of Michotte and of Heider and Simmel. The importance of such phenomena stems in part from the fact that these interpretations seem to be largely perceptual in nature – to be fairly fast, automatic, irresistible and highly stimulus driven – despite the fact that they involve impressions typically associated with higher-level cognitive processing. This research suggests that just as the visual system works to recover the physical structure of the world by inferring properties such as 3-D shape, so too does it work to recover the causal and social structure of the world by inferring properties such as causality and animacy.

Imagine viewing simple movies of the following sort:

(1) Two small squares are sitting in a line, separated by several inches. The first square (A) moves in a straight line until it reaches the second square (B), at which point A stops moving and B starts moving along the same trajectory.

(2) Two small squares are sitting in a line, separated by several inches. The first square (A) begins moving in a straight line towards the second square (B). As soon as A gets close to B, B begins moving quickly away from A in a random direction, until it is again several inches from A, at which point it stops. A continues all the while to move straight towards B's position, wherever that is at any given moment. This pattern repeats several times.

Objectively, all that is happening in such movies is the kinematics described above. Perceptually, however, a striking thing happens: in the first movie, you see A *cause* the motion of B, and in the second movie, you see A and B as *alive*, and perhaps as having certain intentional states, such as A wanting to catch B, and B trying to escape (such movies – and movies of all the figures in this article – can be viewed at http://wjh.harvard.edu/~scholl/demos/Michotte.html). These are examples of what have been called 'functional relations'[1], wherein one perceives various properties in simple displays that are found objectively in neither the actual events themselves nor in their retinal projections.

Such phenomena were first studied in the early 1900s, and later captured the attention of many psychologists with the publication of Michotte's book *The Perception of Causality*[1], and of Heider and Simmel's classical article 'An experimental study of apparent behavior'[2]. The importance of such phenomena stems partially from the fact that although they seem to be largely perceptual in nature – to be fairly fast, automatic, irresistible and highly stimulus-driven – they nevertheless yield impressions such as causality and animacy, which are typically associated with higher-level

cognitive processing. This research suggests that just as the visual system works to recover the physical structure of the world by inferring properties such as 3-D shape, so too does it work to recover the causal and social structure of the world by inferring properties such as causality and animacy.

One especially intriguing aspect of these phenomena is how simple and spare the stimuli can be, with visual displays containing only a few small-moving 2-D geometric shapes. This article focuses on recent work using such displays, and does not discuss other experiments on animacy that have used more specialized stimuli such as faces[3], hands[4] or the biological motion of 'point-light walkers'[5]. It is also restricted to those studies that have investigated the *perception* of causality and animacy. Of course, there is also a wealth of research on when adults and children of all ages will *infer* the existence of a cause or an animate being[6,7]. (This distinction between perceived and inferred causality and animacy is discussed at length in the final section of this article.)
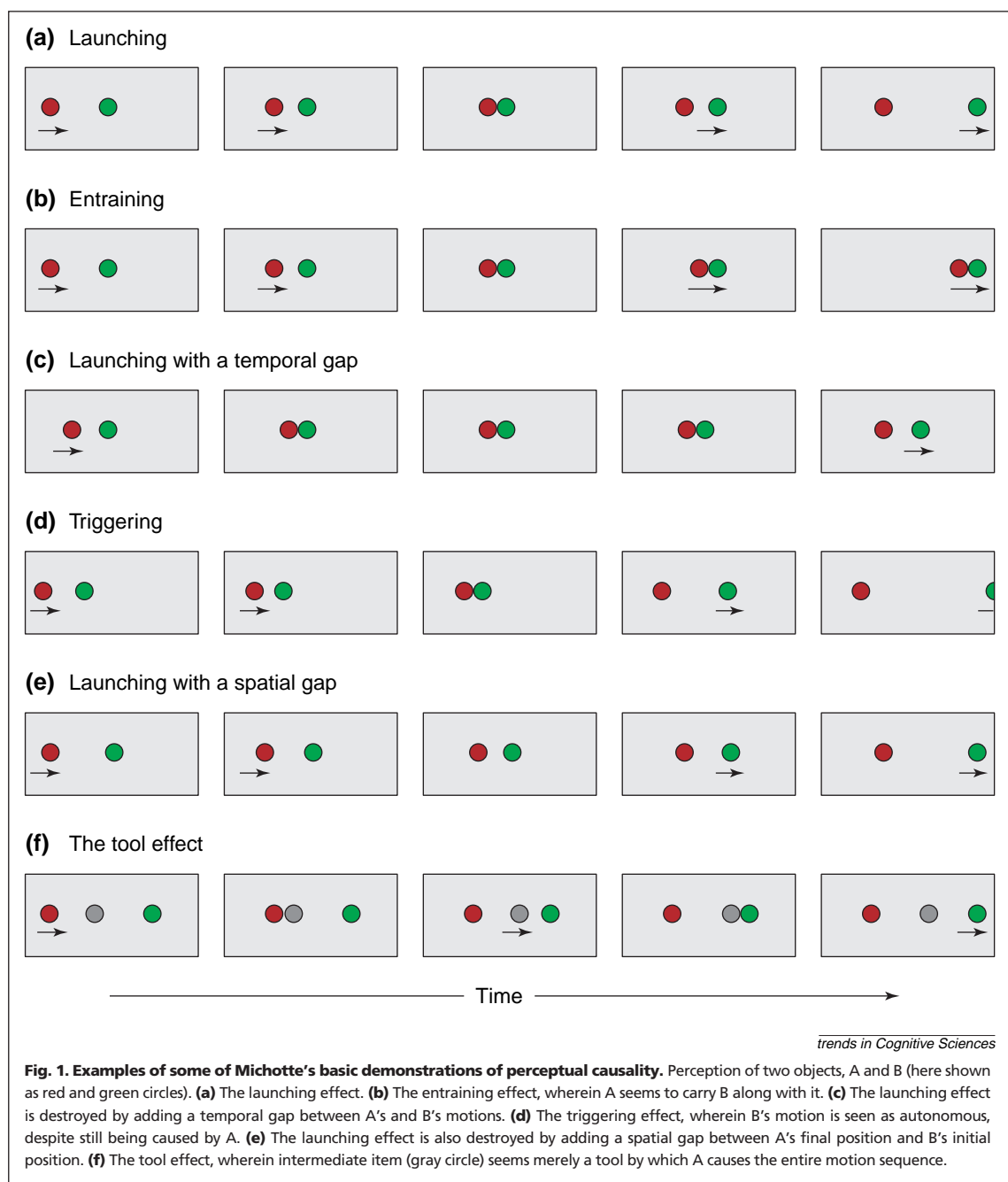
In sum, this article discusses cases in which very simple displays give rise to surprisingly high-level percepts. That perceptual systems can produce such high-level impressions perhaps seems more intuitive when one considers the perceptual recovery of other less exotic properties such as 3-D structure[8]. Some basic visual features (e.g. local orientation) can be recovered fairly directly, whereas others (e.g. depth) cannot be unambiguously extracted from retinal projections without making various other assumptions – for example, the heuristic assumption of rigid objects that the visual system makes in some situations in order to extract structure from motion[9]. Such assumptions often appear to be hardwired into the visual system, and are thus implicit, un-reportable and distinct from higher-level cognitive interpretations[10]. In such cases, methods from psychophysics and experimental psychology can be used to discover these assumptions, and they can be demonstrated in salient ways

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(a) Launching

(b) Entraining

(c) Launching with a temporal gap

(d) Triggering

(e) Launching with a spatial gap

(f) The tool effect

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Fig. 1. Examples of some of Michotte's basic demonstrations of perceptual causality. Perception of two objects, A and B (here shown as red and green circles). **(a)** The launching effect. **(b)** The entraining effect, wherein A seems to carry B along with it. **(c)** The launching effect is destroyed by adding a temporal gap between A's and B's motions. **(d)** The triggering effect, wherein B's motion is seen as autonomous, despite still being caused by A. **(e)** The launching effect is also destroyed by adding a spatial gap between A's final position and B's initial position. **(f)** The tool effect, wherein intermediate item (gray circle) seems merely a tool by which A causes the entire motion sequence.

by using simple schematic displays that satisfy the assumptions in the most minimal way possible. This is what the 'kinetic depth effect'[11] does for the case of computing structure from motion, for instance, and we suggest that this is exactly what Michotte, Heider and their contemporary academic descendants have done for causality and animacy.

The remainder of this article is organized into three sections. In the first, we review contemporary research that has been conducted on perceptual causality. In the second, we review recent research on perceptual animacy. Finally, in the concluding section, we evaluate the evidence for the allegedly perceptual nature of such phenomena.

Perceptual causality
Foundations
The landmark work on the perception of causality was Michotte's book of that name, first published in French in

1946, and later updated and translated into English in 1963 (Ref. 1). (Several of his earlier works on this topic have been translated and gathered together in a more recent collection[12].) Michotte's general strategy was to show observers various simple displays such as those described in the first paragraph of this article, and to record their reported percepts. The observers in Michotte's experiments were not well described, and appear with some exceptions to have consisted of Michotte himself and his close colleagues and students. For this and other reasons, Michotte's methods have received much criticism, some of it rather vigorous and well deserved[13,14], though at least partially explainable in terms of the methodological *zeitgeist* of the day[15,16]. Beyond these early criticisms, it is important to stress that much of the data from the experiments described in this review result from perceptual reports, and are, in this manner, similar to investigations of other subjective visual

phenomena, such as amodal completion or illusory contours. Evidence that such reports reflect perceptual processing un-contaminated by later and higher-level interpretations is discussed in the final section of this article.

Nearly all of Michotte's demonstrations were based on variations of the launching effect described in the opening paragraph of this article: one small object (A) moves until it is adjacent to another item (B), at which point A stops and B starts moving. (Throughout this article, 'A' and 'B' refer to these respective roles.) Such displays give rise to a version of what Michotte called 'phenomenal causality' and what others have termed 'the illusion of causality'[17]: a strong percept that A caused B's motion – that A pushed B, shoved B, 'made it go'. In such cases, B's motion is not perceived as its own, but rather as a simple continuation of A's motion: the percept is of two distinct items but of a single motion that is transferred between them. The bulk of Michotte's demonstrations and most of the early extensions to his work consisted of discovering the spatiotemporal parameters that mediate these causal percepts, such as the items' relative speeds, speed–mass interactions[8,18], overall path lengths, and spatial and temporal gaps. Perhaps the most crucial result, however, is simply that there are such precise conditions: these percepts seem to be largely stimulus driven, and objectively small manipulations to the displays can cause the causal nature of the percepts to disappear. Figure 1 portrays these basic effects and some of the manipulations explored by Michotte. (Note that the dynamic nature of these displays is crucial to the robust percepts, as can be seen in the online movies.)

Several researchers following Michotte attempted to tone down some of his stronger claims. Michotte implied that his effects were seen for all observers immediately, but others have demonstrated that only 65% to 85% of observers report the basic launching percept upon its first presentation[13,19–21]. Similarly, others have demonstrated that the robustness of the reports of causal percepts can be altered with practice, for example by varying the number of highly causal or highly non-causal intervening displays before the test displays[22,23]. However, as others have indicated, many such manipulations might affect response biases rather than the actual percepts[24]. And, as stressed by White[21], such amendments to Michotte's strong claims should not distract us from the existence of the phenomena in the first place: 'The remarkable thing…is that causal processing is sufficiently irresistible to occur at all with such imperfect stimuli'.
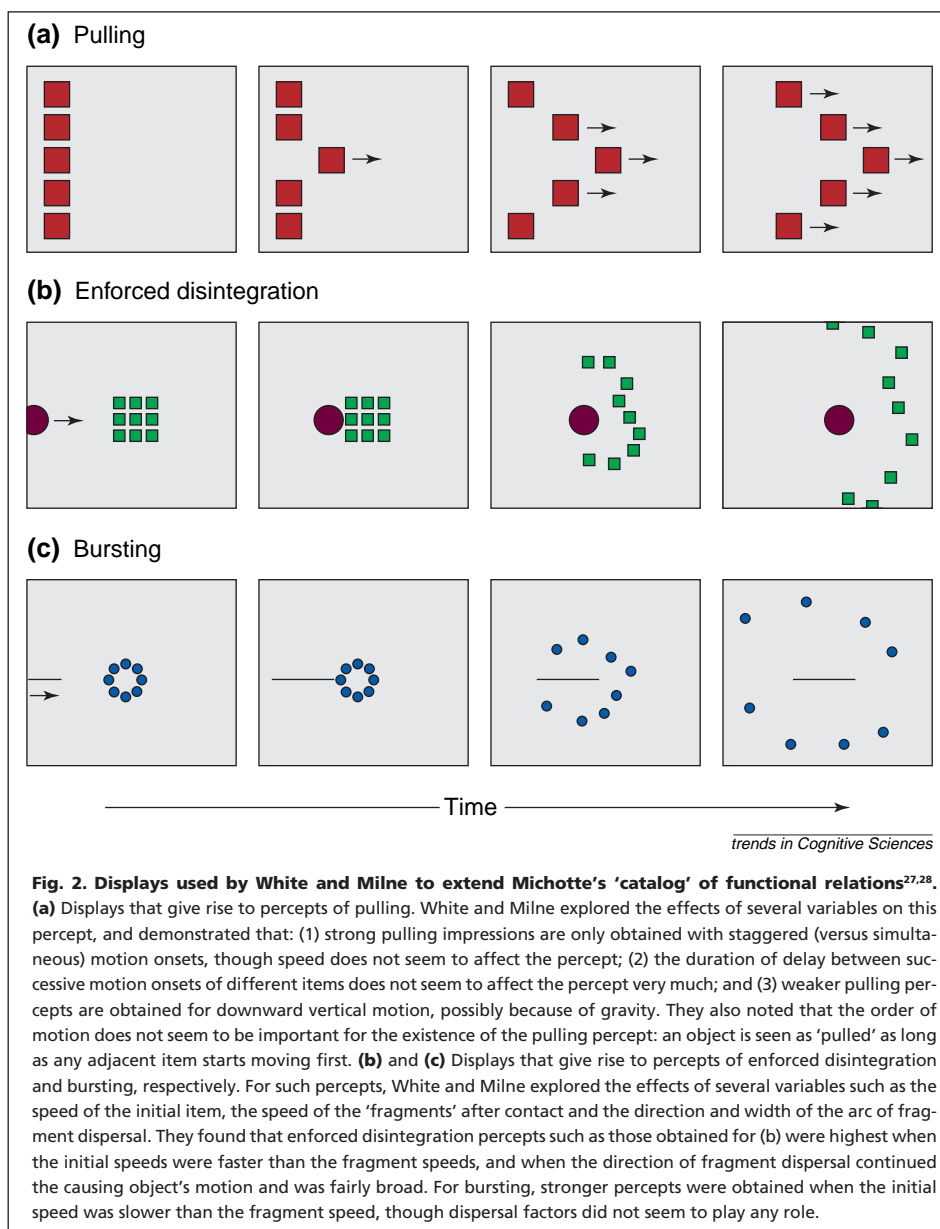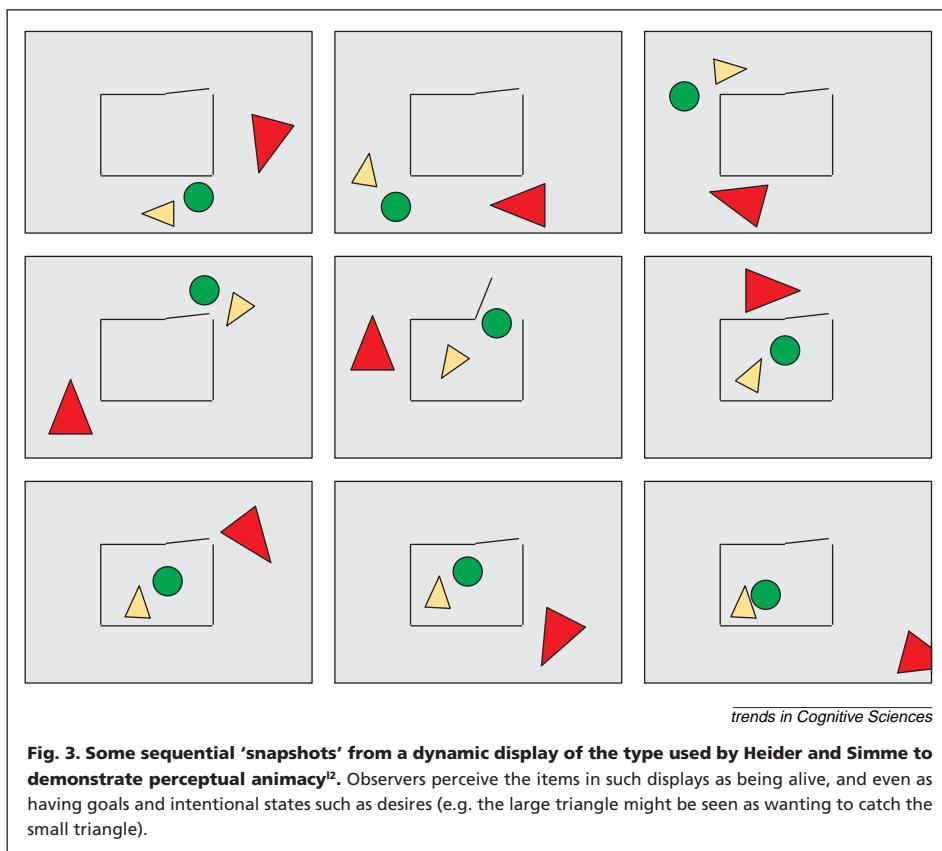

Fig. 2. Displays used by White and Milne to extend Michotte's 'catalog' of functional relations[27,28]. **(a)** Displays that give rise to percepts of pulling. White and Milne explored the effects of several variables on this percept, and demonstrated that: (1) strong pulling impressions are only obtained with staggered (versus simultaneous) motion onsets, though speed does not seem to affect the percept; (2) the duration of delay between successive motion onsets of different items does not seem to affect the percept very much; and (3) weaker pulling percepts are obtained for downward vertical motion, possibly because of gravity. They also noted that the order of motion does not seem to be important for the existence of the pulling percept: an object is seen as 'pulled' as long as any adjacent item starts moving first. **(b)** and **(c)** Displays that give rise to percepts of enforced disintegration and bursting, respectively. For such percepts, White and Milne explored the effects of several variables such as the speed of the initial item, the speed of the 'fragments' after contact and the direction and width of the arc of fragment dispersal. They found that enforced disintegration percepts such as those obtained for (b) were highest when the initial speeds were faster than the fragment speeds, and when the direction of fragment dispersal continued the causing object's motion and was fairly broad. For bursting, stronger percepts were obtained when the initial speed was slower than the fragment speed, though dispersal factors did not seem to play any role.

Contemporary studies

Much of the contemporary research on perceptual causality has attempted to generalize the basic phenomena in various ways. For example, it has been demonstrated that the launching effect replicates with other types of stimuli, including apparent motion rather than real motion[17], and that such percepts seems to be culturally universal[25,26]. In Morris and Peng's experiments[25], American and Chinese observers' percepts of launching displays did not differ, despite the fact that these two groups had massively different patterns of higher-level causal attribution.

Several other researchers have extended Michotte's studies both by continuing his exploration of the mediating spatiotemporal variables, and by extending the 'catalog' of 'functional relations' to include other phenomena. For example, White and Milne created various simple displays that gave rise to the robust percept that one object was pulling another[27] (conceptually similar to Michotte's 'traction' experiments). An example of such a stimulus is shown in Fig. 2a. Here, the middle object, which moves first, is seen to pull the others

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Fig. 3. Some sequential 'snapshots' from a dynamic display of the type used by Heider and Simme to demonstrate perceptual animacy[12]. Observers perceive the items in such displays as being alive, and even as having goals and intentional states such as desires (e.g. the large triangle might be seen as wanting to catch the small triangle).

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along. As in the launching display, observers see multiple objects but only a single motion, which is phenomenally duplicated in all of the items. Note, however, that this display does not satisfy the requirements for launching itself: the initial object actually moves away from the other items, and at no time do two items ever contact each other. In a related study, White and Milne carried out similar investigations of percepts they termed enforced disintegration and bursting[28] (see Fig. 2b,c), similar to Michotte's triggering percepts in launching displays. In each display, one item travels until it contacts a group of additional items, at which point they begin moving with various speeds and in various directions. Subjects perceive such displays in terms of salient categories such as bursting. The pattern of mediating variables here is again fairly complex, but the striking and important finding is just that, as with launching and entraining, these additional causal percepts seem to be salient, immediate and irresistible, despite the fact that they involve only geometric figures on a computer screen. (Note, though, that although these phenomena are clearly causal and embody additional types of 'functional relations', they might not count as demonstrations of phenomenal causality *per se* under Michotte's strictest definition, wherein the existence of only a single 'amplied' motion in an event is crucial.)

In all of their experiments, White and Milne used Natsoulas' method of rating three different statements for each display[29], which emphasize a percept of pulling, of no interaction, and of items moving on their own accord. This contrasts with the bulk of the early research extending Michotte's studies, which involved obtaining direct perceptual reports. Both methods allow for effects to creep in at the response bias stage, but are essentially ways of quantifying the qualitative perceptual experience, as is carried out in demonstrations of many

other subjective visual phenomena such as amodal completions or illusory contours. Moreover, such effects in general seem unlikely to be entirely due to a response bias, because of developmental work showing that the ability to perceive causality from simple motion displays emerges before infants have learned language.

Emergence in infancy

The most compelling evidence that perceptual causality emerges early in life comes from the work of Alan Leslie and his colleagues[30–32]. In his studies, six-month-old infants were habituated to one of several short films based upon Michotte's launching displays. After habituation, infants found a reversal of the film more interesting if they had been habituated to spatiotemporally contiguous launching displays (see Fig. 1a) than if they had been habituated to displays with spatial or temporal gaps that degrade the causal percept in adults (see Fig. 1c,e). Leslie argues that the six-month-olds looked longer at reversed contiguous displays (compared with reversed displays with spatial or temporal gaps), because, although all displays involved reversed kinematics, only the reversed contiguous display (Fig. 1a) involved an additional change in the causal roles (i.e. which shape is the 'hitter' and which is the 'hittee'). In short, Leslie and his colleagues showed that six-month-olds perceive causality when shown launching displays similar to those that produce causal percept in adults[32]; later developmental studies have supported and refined this picture[33–38].

Perceptual animacy

From the beginning, researchers have emphasized that the property of animacy also appears to be perceived in simple displays[2,39]. Michotte even suggested that simple motion cues provide the foundation for social perception in general: 'In ordinary life, the specifying factors – gestures, facial expressions, speech – are innumerable and can be differentiated by an infinity of nuances. But they are all additional refinements compared with the key factors, which are the simple kinetic structures'[39]. The studies of perceptual animacy discussed below involve at least the perception of a simple shape's being alive; in addition, many of them go even further and employ displays that give rise to the perception of goals (e.g. 'trying to get over here') and even mental states (e.g. 'wanting to get over there'). Though there might be important gradations of these types in animacy percepts, they are not discussed here, and all such phenomena are referred to as demonstrations of perceptual animacy. (For a discussion of such gradations – and, in particular, one that characterizes the goal-directedness as more primary than the perception of a self-propelled or living element – see the recent papers by Csibra, Gergely and colleagues[40,41].)

Heider and Simmel created a film showing three geometric figures (a large triangle, a small triangle and a small

circle) moving in the vicinity of a rectangle[2] (see Fig. 3, and the movie clip online). Although static clips of the film conveyed little information about the properties of the circle and triangles, after viewing the animation observers were remarkably consistent when asked to describe the objects. Observers attributed personality traits (e.g. shyness, being a bully) and emotions (e.g. frustration, anger) to the geometric figures, regardless of the instructions they were given. Heider and Simmel explained these findings by asserting that temporal contiguity and spatial proximity produced phenomenal relationships among the geometric figures.

Since Heider and Simmel's original experiment, a large number of follow-up studies have assessed the generality and robustness of such phenomena[42]. Early work suggesting that the perception of animacy is context sensitive involved priming the subjects with emotional information[43] or giving the moving shapes little iconic facial expressions[44]. This work was inconclusive, however, as the priming study introduced salient task demands, whereas the facial expressions probably engaged distinct specialized recognition processes. Moreover, others have demonstrated that the specific animate descriptions given to such displays are remarkably consistent across a wide range of cultures[25,26,45], and developmental research has shown that three- and four-year-olds also attribute desires, emotions and personalities to the geometric shapes in Heider and Simmel's animation[46].

Other developmental work has revealed that children will interpret simple geometric shapes as intentional agents based upon their movement patterns[40,41,47,48]. Gergely, Csibra and their colleagues, for instance, have used displays such as those in Fig. 4 to show that relatively simple motion sequences, which do not rely upon self-initiated movement to cue animacy, can produce an impression of goal-driven behavior in nine-month-old infants[40,41]. Another recent study used this same paradigm to demonstrate that chimpanzees also seem to attribute goals to the items in such displays (see Fig. 4; Ref. 49).

Similarly, Rochat and colleagues report that even three-month-olds preferred to look at displays with two discs engaging in systematic 'social' interaction (chasing) than at displays showing the discs moving independently[50]. It appears that young infants distinguish movements which specify social causality for adults from those which do not. In another study, nine-month-olds were habituated to stimuli containing two non-rigidly moving squares, each modeled after Michotte's 'caterpillar' displays (expanding and contracting squares that yield an impression of self-produced, animate motion in adults). Infants appeared to perceive causality at a distance in their displays – that is, the infants seemed to infer that one square causes movement in the other – without any contact between them[51]. As nine-month-olds understand that inanimate objects cannot act upon one another from a distance, this indicates that these infants must have derived an impression of animacy from the quality of the objects' motions.

Recent research with adults also supports the hypothesis that it is the motion kinematics and not the featural properties of the objects that are largely responsible for perceptual animacy. For example, animacy is perceived even when the simple 'actors' in an animation sequence are groups of items rather than unified shapes[52]. In a more direct contrast between motion information and spatial properties, it was
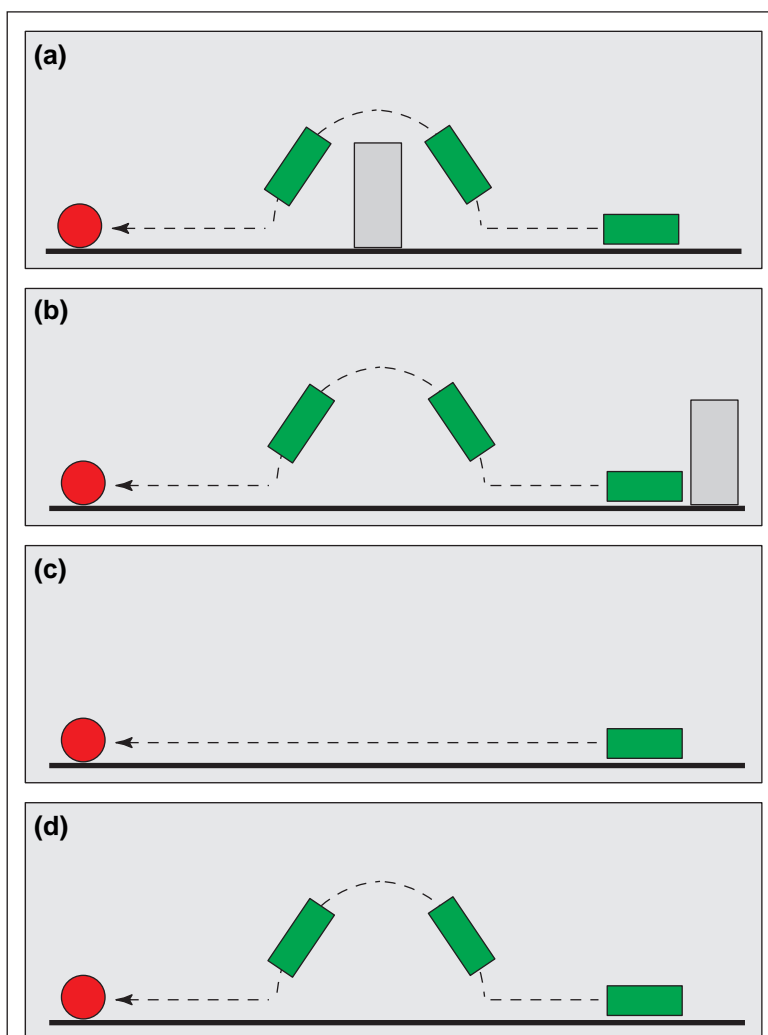
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Fig. 4. Depictions of the displays used to demonstrate that both infants[40,41] and chimpanzees[49] attribute goals to simple shapes in certain dynamic displays. In the studies by Gergely, Csibra and colleagues[40,41], infants as young as nine months were familiarized with either the event depicted in **(a)**, where a rectangle 'jumps' over a barrier on its trajectory towards a circle, or the event depicted in **(b)**, where the rectangle follows the identical trajectory despite the barrier's location off to the side. Following familiarization, infants were tested on displays without a barrier: in the event depicted in **(c)**, the rectangle now moves on a straight linear path towards the circle; in the event depicted in **(d)**, the rectangle continues to follow the same curved path it followed during familiarization trials. Infants who were familiarized with event (a) looked longer at event (d) than at event (c) during test trials, whereas no such difference was observed for infants familiarized to event (b). The authors explain this pattern of results by appeal to the idea that infants interpreted event (a) in goal-directed terms, with the rectangle trying to reach the circle via the most direct unobstructed path. Infants familiarized with event (a) thus found event (c) to be another instance of the same goal-directed event, whereas event (d) was perceived as more novel, despite its greater superficial similarity to the familiarization event (a). Uller and Nichols used this same type of setup and experimental logic (though with slightly different methods) in a looking time study with chimpanzees, and found similar results[49]: the chimpanzees also appeared to attribute goals to the event depicted in (a).

found that a spatially quantized version of the original Heider and Simmel movie (which selectively eliminated featural properties) hardly affected observers' descriptions, whereas a temporally quantized version (which selectively eliminated motion information) resulted in a drastic reduction in reported perceptual animacy[53].

Motion cues

Several researchers have attempted to discover the specific motion cues that mediate perceptual animacy. This research

program began with Bassili, who developed five computer-controlled displays, each showing two circles moving on a dark background[54]. He discovered that a temporal contingency between the changes in direction of two circles produced the percept of an interaction between the figures, and that spatial contingencies influenced the perception of intentionality. Unfortunately, his subjects' ratings of animacy were highly variable, suggesting that different observers used different cues to perceptual animacy.

More recent research has also explored the relationship between the perception of interaction, intention, and animacy. Dittrich and Lea presented adult subjects with displays containing several randomly moving letters (distractors) and a target letter whose movement was designed to simulate biologically meaningful, intentional motion – either predatory stalking or following a parent to keep from getting lost[55]. (The second 'movie' from the opening paragraph of this article is modeled on these displays.) Dittrich and Lea varied the number of moving elements, the directness of movement of the distractors (maximum angle of direction change between cycles), the speed of the distractors (maximum movement between cycles), the directness of the target (maximum angular deviation from a perfectly 'heat-seeking' path towards one of the distractors chosen as a 'sheep' to the target's 'wolf'), the speed of the target, and the 'relentlessness' of the target (minimum movement between cycles). After viewing each display, subjects were asked to identify which one of the characters 'was different from the others', and then to rate the degree to which the selected letter appeared to be doing something purposeful, how much it interacted with other letters and to what extent it simulated an animate creature.

Dittrich and Lea concluded that perceiving a target's movement to be animate motion depended on both the degree to which there appeared to be an interaction between the target and its goal, and the impression of intentionality produced by the movement. In addition, their data indicated that the perception of interaction depends upon the relationship between the trajectory of the target and the trajectories of the distractors, and that the perception of intentionality depends upon the trajectory of the target. More specifically, their observers reported more intentional percepts from displays in which the target's motion was more direct, and were better at detecting the 'target' object when it moved faster than the distractors. Finally, causing the target's 'goal' to be invisible impaired but did not abolish the perceptual animacy.

Stewart also set out to investigate how motion influences the perception of animacy (discussed in Ref. 55). Her investigation was guided by a specific hypothesis: observers should describe an object as animate whenever its motion 'violates Newtonian laws'. Technically, motions cannot violate Newtonian laws (except for relativistic effects); however, it is clear that what Stewart actually meant was that motions that would require a moving body to have access to a hidden energy source (e.g. smooth accelerations or sudden stops) would be perceived as animate. She tested this idea, which we will refer to as the 'energy violation' hypothesis, by presenting subjects with several computer-generated displays showing a single ball moving in the vicinity of static bars that were intended to be interpreted as obstacles and boundaries. Although some of Stewart's findings were consistent with

her expectations, many of the motion paths that the energy violation hypothesis predicts will be perceived as animate were ambiguous: some of Stewart's subjects saw them as inanimate and some saw them as animate. Only three types of motion consistently produced animate percepts: starts from rest, changes in direction to avoid a collision and direct movement towards a goal. As discussed below, however, such effects are clearly mediated by other contextual factors; if this were not the case, observers should report that the first items in most launching displays (Fig. 1a) look animate, which they do not.

In a series of follow-up experiments, Gelman and colleagues replicated and extended Stewart's findings[56]. They presented subjects with several computer-generated displays, showing one or two small balls moving in 'environments' of static lines and geometric shapes. These displays varied in terms of the shapes of trajectories, the presence or absence of a second ball and the type of environment. Gelman *et al.* reported that observers favored animate interpretations in environments where the balls' movements were consistent with some aspect of the environment representing either an obstacle or a goal. By contrast, observers favored inanimate interpretations when balls moved in 'odd' environments or when no environmental information was given. These findings led Gelman and colleagues to suggest that the ability to classify objects into animates and inanimates is not based solely on perceptual information, but also draws upon innate or early-developing knowledge of causal principles (a suggestion that contrasts with other conclusions, as is discussed again below). By contrast, Blythe and colleagues have argued that a small set of motion cues can be sufficient not only to determine whether or not a moving object is animate, but also to determine what intention motivated the object's movement[57]. They present an algorithm that uses seven motion cues to predict observers' responses when asked to assign displays to one of six intentional categories. They then go on to suggest that people and other animals might use an algorithm such as this to infer the intentions of moving entities. This work is important when one considers that many other researchers have focused on the perception of intention from motion when viewing such displays[40,41,54–56,58].

Cues mediating the perception of animacy in simple displays

In general, the displays used to investigate the perception of animacy and the perception of intentionality have been longer, have had more complex trajectories and/or have had more complex environments (which might include moving elements) than the displays used to investigate the perception of causality. This has made it difficult to conduct a rigorous analysis of the mediating factors of perceptual animacy (similar to the one conducted by Michotte and others for perceptual causality). However, Tremoulet and Feldman have recently made progress in this direction[59]. They created extremely simple stimuli showing a single white particle moving across a featureless dark background (see Fig. 5 for details). In cases where the trajectories were the same, other factors such as the local orientation of the particles throughout their trajectories impacted the strength of the resulting animacy percepts – a result that refutes the notion that perceiving energy violations is all there is to perceiving animacy.

The most important contribution of Tremoulet and Feldman's recent study is not its refutation of the 'energy violation' hypothesis, however, but rather its demonstration that the combination of two extremely simple, highly perceptible motions (change in speed and change in direction) can produce an impression of animacy, even when presented in a featureless background. Follow-up experiments suggest that this extremely simple motion path might convey intentionality despite the absence of a goal or context; if a single static dot is added to the backgrounds of these displays, the strength of the animacy percept depends upon the location of the dot (this replicates the finding of Gelman and colleagues that the visual environment can influence the perception of animacy). More research is underway to investigate how context and motion interact to create an impression of animacy.

Initial evidence from cognitive neuroscience

Other very recent studies have addressed perceptual animacy using tools drawn from cognitive neuroscience, and have begun to link such phenomena more closely to the underlying brain structures. Heberlein and colleagues showed the original Heider and Simmel movie to a patient with amygdala damage, who (unlike normal observers and other brain-damaged controls) did not describe them using any social or anthropomorphic terms[60]. This supports the idea that the amygdala is a crucial part of the system that mediates social perception[61]. Happé and Frith[62] have also made a first attempt to localize perceptual animacy in the brain using neuroimaging techniques. They conducted a PET study using these types of display, contrasting random movement with goal-directed movement (e.g. chasing) and intentional movement (e.g. mocking), and found that these latter displays elicited more activity than the random-movement displays in the temporoparietal junction, fusiform gyrus, occipital gyrus and medial frontal cortex.

A link between perceptual and cognitive processing?

Having reviewed the recent empirical work on the nature of perceptual causality and animacy, we now address the allegedly perceptual nature of these phenomena more directly. As noted above, one of the reasons that such phenomena are interesting is that they both have the character of visual percepts yet involve what are traditionally thought to be higher-level concepts. Without this perceptual nature, these phenomena are of much less interest. After all, it is of no great surprise that one can *conceive* of some visual object as causing some action, as animate, or as anything you wish. But to the degree that such phenomena reflect perceptual processing, their existence is more interesting: they suggest that perceptual processes have more to do with domains previously considered to be purely cognitive.

Most of the controversy surrounding perceptual causality and animacy has focused on whether such processing can be

considered innate. Michotte, for instance, frequently downplayed experiential effects when discussing perceptual causality, citing as evidence the universality of the percepts, their seeming encapsulation from higher order interpretations (what he called 'negative' and 'paradoxical' cases), and the high correlation between the character of the stimuli and the resulting percepts, with 'the distribution of response frequencies generally showing the usual pattern for psychophysical functions. In the case of acquired meaning…the link between stimulation and response is usually much weaker'[63]. Some contemporary researchers have supported this position[32,35,48,64], whereas others have argued that the evidence for innateness is inconclusive[6,8,27,38]. This controversy will not be reviewed here, however, as the frequent discussion of innateness has often been an illfitting stand-in for the perceptual nature of these phenomena (for reasons discussed below). We will simply conclude that the issue is unresolved, noting only that experiential effects might often be localized to response biases (see Schlottman and Anderson[24] for a discussion of several subtleties), and that in general the existence of an innate origin is quite compatible with a wide variety of experiential and developmental effects[65].

Modular processing

Rather than focusing on innateness as a substitute for the perceptual nature of these phenomena, we suggest that this issue might be better characterized by appeal to the notion of modularity. Modules, as discussed by Fodor[66], are special-purpose mechanisms – parts of the mind, analogous to organs of the body – that are characterized by restrictions on information flow. On the one hand, a module's processing is encapsulated from external information, so that, for example, learning that the Müller-Lyer illusion is an illusion does not cause it to go away, because the visual mechanisms that construct the percept are encapsulated from that belief.
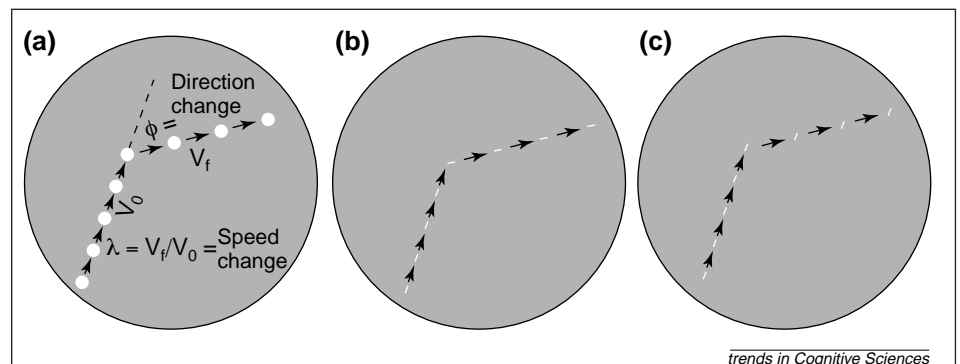

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Fig. 5. Examples of the three particle types used in displays created by Tremoulet and Feldman to investigate the minimal conditions for perceptual animacy[59]. The particles' motion paths were short and uncomplicated: initially, a particle moved in a random direction at a constant speed for 375 ms, then it simultaneously changed both speed and direction, and continued at the new speed in the new direction for another 375 ms. Three different particle types were compared: **(a)** a simple circle (the 'dot condition'); **(b)** a rectangle which changed orientation as it changed direction, so its principal axis was always aligned with the direction of motion (the 'aligned' condition); and **(c)** a rectangle that started out aligned with the direction of motion, but did not change orientation as it changed direction (the 'misaligned' condition). Particles in (b) appeared most animate, followed by particles in (a). In both these conditions, the impression of animacy grew stronger with increases in angle of direction change (ϕ) and increases in final speed (V_f). By contrast, particles in (c) did not look animate to most observers. Corresponding displays from (a) and (c) (that is, displays with the same speed and direction changes) always contained precisely the same motion paths [whereas the corresponding display from (b) might have included a rotation]. Thus, all increases in energy contained in display in (a) were also contained in the corresponding display in (c). However, observers rated the particles in (a) as more likely to be animate than the particles in (c). Therefore, there must be more to inferring animacy than simply perceiving increases in energy.

On the other hand, external processes receive a module's output, but cannot get inside to the 'interlevels' of processing: this can explain, for instance, why we easily recognize objects and faces without any insight into how we do so. Because of such restrictions, modules are typically fast, automatic, mandatory and are often innately specified[66,67]. Note, however, that modules need not be innate! In addition to both the fact that modules might require environmental 'triggering' to come online and the possibility that modules might develop from 'scratch' over time, based on experience[68], Scholl and Leslie note that there is nothing in the notion of modularity to prevent a module from tuning itself on the basis of the information that does characterize its input[65]: the essence of modularity identifies restrictions on information flow to and from the module, but places no restrictions on what a module does internally with the information it does receive. (This is one point that speaks against those theorists who argue against modularity simply on the basis of an observable instance of development[38].) Modules can thus be innate, acquired or some mixture thereof, and to the extent that the notion of modularity captures the 'perceptual' nature of these phenomena, debates about innateness prove irrelevant.

To what degree do phenomena of perceptual causality and animacy appear to reflect modular perceptual processing? To begin with, these phenomena do seem to enjoy most of the traditional 'symptoms' of modularity. They are domain-specific by definition, in that they result in specific causal and intentional interpretations (i.e. they give rise to only a few qualitatively separate types of percepts). They are also entirely visual phenomena (though it is an interesting question whether similar effects might be observable in other modalities). Precisely what visual information serves as the input to such a module remains to be determined. The results of Gelman and colleagues discussed above[56] suggest that the computation of animacy is carried out 'not by motion alone', although we would argue that the additional contextual factors might still be visually (and not conceptually) derived. The timecourse of such phenomena is very fast: phenomenologically these causal and animate percepts occur nearly instantaneously upon viewing the displays. They are also mandatory in the way that most visual illusions are: to the degree that the events are clearly perceived (perhaps attended and/or fixated[69]), the causal or animate nature of the resulting percepts is nearly irresistible. This reflects a type of encapsulation: despite the fact that observers know that the displays are not really causal or animate, this knowledge does not appear to be taken into account by the mechanisms that construct the percepts. Conversely, higher-level external processes do not seem to have access to the 'interlevels' of this processing: we are greeted with causal percepts when viewing launching displays, for instance, without any ability to determine how they came about. Like recognizing speech or recognizing a face, recognizing physical causality in such situations seems phenomenologically just to 'happen' quite automatically.

Automaticity
Michotte referred to this as the 'immediacy' of the percepts, and indeed he stressed most of these hallmarks of modularity in his writings[1,39,63]: '[T]his is not just a "meaning" attributed to the literal, step-by-step translation of a table of stimuli; they

are primitive specific impressions which arise in the perceptual field itself'. More contemporary research also supports this view. For instance, Dittrich and Lea stress the apparently mandatory and data-driven nature of the percepts in their displays[55]. They note that '[T]he instructions given to the subjects made very little difference to any dependent measure, while virtually all parameters of motion had some straightforward effects', and they conclude that 'The immediate impression of intentionality (or causality) is given by a "bottom-up" process of selecting specific motion features'. It is important to realize, however, that this automaticity and irresistibility might often depend on clearly perceiving and perhaps attending to the event. For example, infants' attention can be distracted from the relevant event in launching displays when multiple featurally complex objects are used[33,34,36,38].

White stresses the speed of perceptual causality[21]. His thesis is that all of the important processing with regard to such stimuli integrates over less than 250 ms in a chunk at the 'iconic' stage, and is therefore 'automatic' rather than 'controlled' (in the sense of Shiffrin and Schneider[70]). Similarly, Premack argues that 'the infant's concept [of intention] is an automatic reading of a perceptual input'[48], based on the detection of self-propulsion. Blythe and colleagues propose that humans rely upon a simple innate heuristic that automatically determines the intentions of moving agents[57]; effectively, they too claim that observers automatically perceive intention in motion. One remaining problem for such claims of automaticity is the fact (described above) that there are considerable individual differences in the rates of reported perceptual causality and animacy upon the very first presentations of typical displays. Existing accounts involving automaticity have failed to address such data, and to address empirically the suspicion that such differences are due to some subjects reporting more considered interpretations of the displays rather than their percepts. (Michotte noted, however, that even observers who do not perceive causality upon their first encounter with a launching event will do so spontaneously after repeated presentations, and do not require any explicit instruction[1].)

Leslie has worked out the most explicit proposal for a modular basis for perceptual causality[64,71]. He notes that 'To suggest that there is such a thing as a perceptual illusion of causality is to imply that there is a rather humble perceptual mechanism operating automatically and incorrigibly upon the spatio-temporal properties of events yet producing abstract descriptions of their causal structure…Taking input from lower level motion-processing, this device will parse submovements, produce higher-level descriptions of the spatio-temporal properties of the event, and produce a description of its causal structure'[64]. (For further details of Leslie's theory, see Refs 31,32,35,64,71.) Of course, many important unanswered questions remain about the nature of such a mechanism. What, for instance, is the format of the 'causal' interpretation that results from such processing? Is such a mechanism simply wired to return an explicit causal description of the event, similar in format to that which might be obtained by higher-level and more domain-general reflection? Or, is the causal interpretation generated in the way that an interpretation of depth might be generated, in an entirely visuospatial format?

Some of the most direct evidence for automaticity and encapsulation comes from the recent work of Anne Schlottmann and her colleagues, who have directly contrasted causal perception and causal inference[72,73]. In one study, Schlottmann and Shanks[72] studied such issues in launching displays by testing whether factors known to affect causal inference also affected causal percepts. In assessing causation between some pair of events A and B, the existence of a third event C that better co-varies with B will steal the 'judged cause' of B away from A. Schlottmann and Shanks implemented such a situation in a launching event, where the additional co-variate was a brief and momentary color change, the end of which always coincided with the movement of B. B moved on every trial following this color change, which was also sometimes – but not always – correlated with A's arrival. With careful instructions distinguishing perceived and judged causality, they found that the color change had no effect on the perceived causality: despite the imperfect correlation, the perceived cause of B's movement was always the arrival of A when it did correlate. In explicit judgments, by contrast, the existence of the easily perceived higher correlation with color change led to the inference that B's motion was in fact caused by the color change. In general, they noted that the 'factors that influence judgments of causality have no detectable effect on the perception of causality in launch events'.

Conclusions

The available evidence concerning the perception of causality and animacy is largely consistent with the view that such phenomena reflect primarily perceptual and perhaps modular processing, and at a minimum are very different (and can be dissociated) from high-level cognitive judgments of the existence of causality or animacy. This view can be seen as an updated version of the classical theories of such phenomena (including Michotte's theory), and it contrasts with many other recent views[6,8,24,38,56,74]. White takes a contrasting view in a recent book, and argues against a modular interpretation by appeal to the lack of ecological validity in most of these experiments[6]: 'It does not seem likely that there would be an inbuilt visual mechanism for perceiving event sequences that would rarely if ever be encountered in a natural, as opposed to human-made, environment'. But such a mechanism presumably does work in naturalistic events. The situation might be entirely analogous to less controversial processes, such as the extraction of structure from motion. Here is a case where the visual system appears to make hardwired and plausibly innate assumptions about the world, which vision scientists have uncovered and made salient in simple 'toy' displays, such as the kinetic depth effect, which satisfy the built-in assumptions in as minimal a way as possible. Michotte, Heider and their contemporary academic descendants have done the same thing for causality and animacy: they have used 'toy' displays to eliminate confounding noise, and to distill the precise rules that the visual system appears to use when recovering the causal and social structure of the world.

This article has attempted to review recent evidence for what such rules might look like, and to discuss their nature and relation to perceptual and cognitive processing. The phenomena of perceptual causality and animacy might indeed reflect some specialized perceptual processing that is not easily 'pene-

Outstanding questions

- What is the relationship between perceptual causality and perceptual animacy, which have been treated together in this article? Are they mediated by the same mechanisms or by distinct mechanisms that work on similar principles? Are they mediated by the same or separate brain areas? Additional neuroimaging research could perhaps address these questions.
- More generally, are perceptual causality and animacy part of a larger integrated system of social perception, or are they relatively isolated instances of more specific perceptual heuristics?
- What is the relationship of attention to the phenomena discussed here? Cavanagh and colleagues have recently demonstrated that attention is necessary to perceive biological motion and other simple perceptual events[75]. Is attention necessary to perceive causality and animacy? Are causality and animacy evident in a noisy display even when attention is otherwise distracted? To what degree will animate objects capture attention? Similarly, might eye movements play a mediating role in the perception of causality and animacy[69]? The answers to these questions are the topic of our current research.
- More specifically, how might these phenomena be represented on the level of object-based attention, by mechanisms such as object files or object indexes[76,77]? Could such a level of representation explain the details of the 'launching' percepts?
- To the degree that these phenomena appear to be modular in nature, we might expect them to be independently disruptible by brain damage or strokes. Are there any neuropsychological syndromes that involve such deficits?
- Do animals other than humans also perceive causality and animacy in all the same situations, and based on the same stimulus factors? Studies have now begun to look at animacy in non-human primates[49,78], but it remains to be seen how much such initial results will generalize to other species and other stimuli. One writer has suggested that only tool-making species will evidence perceptual causality[79].
- All of the phenomena discussed here occur in the visual domain. Are there any auditory or tactile analogues of perceptual causality or animacy?

trated' by higher-level cognition. In this sense, such phenomena are of interest in that they lie at an intersection of perceptual and cognitive processing, where simple schematic displays are parsed via perceptual systems in causal, animate or even intentional terms – properties traditionally associated with higher-level cognitive processing. The continued study of these phenomena will help elucidate the scope of perceptual processing, and much work remains to be done (see Outstanding questions). Indeed, rarely in experimental psychology or vision science has such a rich set of phenomena been so understudied. This is at least partially attributable to the technical difficulty in the past of working with such dynamic displays, but today such displays are trivially easy to generate, and in the near future it should be possible to characterize comprehensively the precise stimulus conditions that give rise to these percepts in order to discover the perceptual 'grammar' of causality and animacy.

References

1 Michotte, A. (1946/ English transl. 1963) *The Perception of Causality*, Basic Books
2 Heider, F. and Simmel, M. (1944) An experimental study of apparent behavior. *Am. J. Psychol.* 57, 243–249

3 Cole, J. (1999) *About Face*, MIT Press

4 Leslie, A.M. (1984) Infant perception of a manual pick-up event. *Br. J. Dev. Psychol.* 2, 19–32

5 Johansson, G. (1973) Visual perception of biological motion and a model for its analysis. *Percept. Psychophys.* 14, 201–211

6 White, P.A. (1995) *The Understanding of Causation and the Production of Action*, Erlbaum

7 Gelman, R. (1990) First principles organize attention to and learning about relevant data: number and the animate-inanimate distinction as examples. *Cognit. Sci.* 14, 79–106

8 Runeson, S. (1983) On visual perception of dynamic events. *Acta Universitatis Upsaliensis: Studia Psychologica Upsaliensia*, Uppsala, Sweden

9 Ullman, S. (1979) The interpretation of structure from motion. *Proc. R. Soc. London Ser. B* 203, 405–426

10 Pylyshyn, Z.W. (1999) Is vision continuous with cognition? The case for cognitive impenetrability of visual perception. *Behav. Brain Sci.* 22, 341–423

11 Wallach, H. and O'Connell, D. (1953) The kinetic depth effect. *J. Exp. Psychol.* 45, 2015–2017

12 Thinès, G. *et al.*, eds (1991) *Michotte's Experimental Phenomenology of Perception*, Erlbaum

13 Boyle, D. (1960) A contribution to the study of phenomenal causation. *Q. J. Exp. Psychol.* 12, 171–179

14 Joynson, R.B. (1971) Michotte's experimental methods. *Br. J. Psychol.* 62, 293–302

15 Costall, A. (1991) Phenomenal causality. In *Michotte's Experimental Phenomenology of Perception* (Thinès, G. *et al.*, eds), pp. 51–64, Erlbaum

16 Montpellier, G. and Nuttin, J. (1973) A note on 'Michotte's experimental methods' and 'Michotte's ideas'. *Br. J. Psychol.* 64, 287–289

17 Gordon, I. *et al.* (1990) Perceived causality occurs with stroboscopic movement of one or both stimulus elements. *Perception* 19, 17–20

18 Hecht, H. (1996) Heuristics and invariants in dynamic event perception: immunized concepts or non-statements? *Psychonomic Bull. Rev.* 3, 61–70

19 Beasley, N. (1968) The extent of individual differences in the perception of causality. *Can. J. Psychol.* 22, 399–407

20 Gemelli, A. and Cappellini, A. (1958) The influence of the subject's attitude in perception. *Acta Psychol.* 14, 12–23

21 White, P.A. (1988) Causal processing: origins and development. *Psychol. Bull.* 104, 36–52

22 Gruber, H. *et al.* (1957) Effects of experience on perception of causality. *J. Exp. Psychol.* 53, 89–93

23 Powesland, P.F. (1959) The effect of practice upon the perception of causality. *Can. J. Psychol.* 13, 155–168

24 Schlottman, A. and Anderson, N.H. (1993) An information integration approach to phenomenal causality. *Mem. Cognit.* 21, 785–201

25 Morris, M.W. and Peng, K. (1994) Culture and cause: American and Chinese attributions for social and physical events. *J. Personal. Soc. Psychol.* 67, 949–971

26 Rimé, B. *et al.* (1985) The perception of interpersonal emotions originated by patterns of movement. *Motiv. Emotion* 9, 241–260

27 White, P.A. and Milne, A. (1997) Phenomenal causality: impressions of pulling in the visual perception of objects in motion. *Am. J. Psychol.* 110, 573–602

28 White, P.A. and Milne, A. (1999) Impressions of enforced disintegration and bursting in the visual perception of collision events. *J. Exp. Psychol. Gen.* 128, 499–516

29 Natsoulas, T. (1961) Principles of momentum and kinetic energy in the perception of causality. *Am. J. Psychol.* 74, 394–402

30 Leslie, A.M. (1982) The perception of causality in infants. *Perception* 11, 173–186

31 Leslie, A.M. (1984) Spatiotemporal continuity and the perception of causality in infants. *Perception* 13, 287–305

32 Leslie, A.M. and Keeble, S. (1987) Do six-month-old infants perceive causality? *Cognition* 25, 265–288

33 Oakes, L. and Cohen, L. (1990) Infant perception of a causal event. *Cognit. Dev.* 5, 193–207

34 Cohen, L. and Oakes, L. (1993) How infants perceive a simple causal event. *Dev. Psychol.* 29, 421–432

35 Leslie, A.M. (1994) ToMM, ToBy, and agency: core architecture and domain specificity. In *Mapping the Mind: Domain Specificity in Cognition and Culture* (Hirschfield, L. and Gelman, S., eds), pp. 119–148, Cambridge University Press

36 Oakes, L. (1994) Development of infants' use of continuity cues in their perception of causality. *Dev. Psychol.* 30, 869–879

37 Baillargeon, R. *et al.* (1995) The acquisition of physical knowledge in infancy. In *Causal Cognition* (Sperber, D. *et al.*, eds), pp. 79–116, Clarendon Press

38 Cohen, L. *et al.* (1998) The development of infant causal perception. In *Perceptual Development: Visual, Auditory, and Speech Perception in Infancy* (Slater, A., ed.), pp. 167–209, Psychology Press

39 Michotte, A. (1950) The emotions regarded as functional connections. In *Feelings and Emotions: The Mooseheart Symposium* (Reymert, M., ed.), pp. 114–125, McGraw-Hill. Reprinted 1991: In *Michotte's Experimental Phenomenology of Perception* (Thinès, G. *et al.*, eds), pp. 103–116, Erlbaum

40 Gergely, G. *et al.* (1995) Taking the intentional stance at 12 months of age. *Cognition* 56, 165–193

41 Csibra, G. *et al.* (1999) Goal attribution without agency cues: the perception of 'pure reason' in infancy. *Cognition* 72, 237–267

42 Kassin, S. (1982) Heider and Simmel revisited: causal attribution and the animated film technique. *Rev. Pers. Soc. Psychol.* 3, 145–169

43 Shor, R. (1957) Effect of preinformation upon human characteristics attributed to animated geometric figures. *J. Abnorm. Soc. Psychol.* 54, 124–126

44 Thayer, S. and Schiff, W. (1969) Stimulus factors in observer judgment of social interaction: facial expression and motion pattern. *Am. J. Psychol.* 82, 73–85

45 Hashimoto, H. (1966) A phenomenal analysis of social perception. *J. Child Dev.* 2, 3–26

46 Berry, D.S. and Springer, K. (1993) Structure, motion, and preschoolers perception of social causality. *Ecol. Psychol.* 5, 273–283

47 Dasser, V. *et al.* (1989) The perception of intention. *Science* 243, 365–367

48 Premack, D. (1990) The infant's theory of self-propelled objects. *Cognition* 36, 1–16

49 Uller, C. and Nichols, S. Goal attribution in chimpanzees. *Cognition* (in press)

50 Rochat, M. *et al.* (1997) Young infants' sensitivity to movement specifying social causality. *Cognit. Dev.* 12, 537–561

51 Schlottman, A. and Surian, L. (1999) Do 9-month-olds perceive causation-at-a-distance? *Perception* 28, 1105–1114

52 Bloom, P. and Veres, C. (1999) The perceived intentionality of groups. *Cognition* 71, B1–B9

53 Berry, D. *et al.* (1992) Effects of disruption of structure and motion on perceptions of social causality. *Pers. Soc. Psychol. Bull.* 18, 237–244

54 Bassilli, J. (1976) Temporal and spatial contingencies in the perception of social events. *J. Pers. Soc. Psychol.* 33, 680–685

55 Dittrich, W. and Lea, S. (1994) Visual perception of intentional motion. *Perception* 23, 253–268

56 Gelman, R. *et al.* (1995) Distinguishing between animates and inanimates: not by motion alone. In *Causal Cognition: A Multidisciplinary Debate* (Sperber, D. *et al.*, eds), pp. 150–184, Clarendon Press

57 Blythe, P. *et al.* (1999) How motion reveals intention: categorizing social interactions. In *Simple Heuristics That Make Us Smart* (Gigerenzer, G. *et al.*, eds), pp. 257–285, Oxford University Press

58 Premack, D. and Premack, A. (1995) Intention as psychological cause. In *Causal Cognition: A Multidisciplinary Debate* (Sperber, D. *et al.*, eds), pp. 185–199, Clarendon Press

59 Tremoulet, P.D. and Feldman, J. Perception of animacy from the motion of a single object. *Perception* (in press)

60 Heberlein, A.S. *et al.* (1998) Impaired attribution of social meanings to abstract dynamic geometric patterns following damage to the amygdala. *Soc. Neurosci. Abstr.* 24, 1176

61 Adolphs, R. *et al.* (1998) The human amygdala in social judgment. *Nature*, 393, 470–474

62 Happé, F. and Frith, U. (1999) How the brain reads the mind. *Neurosci. News* 2, 16–25

63 Michotte, A. and Thinès, G. (1963) La causalité perceptive. *J. Psych. Norm. Pathol.* 60, 9–36. Translated and reprinted 1991: In *Michotte's Experimental Phenomenology of Perception* (Thinès, G. *et al.*, eds), pp. 66–87, Erlbaum

64 Leslie, A.M. (1988) The necessity of illusion. In *Thought Without Language* (Weiskrantz, L., ed.), pp. 185–210, Clarendon Press

65 Scholl, B.J. and Leslie, A.M. (1999) Modularity, development, and 'theory of mind'. *Mind Lang.* 14, 131–153

66 Fodor, J.A. (1983) *The Modularity of Mind*, MIT Press

67 Carston, R. (1996) The architecture of mind: modularity and modularization. In *Cognitive Science: An Introduction* (Green, D. *et al.*, eds), pp. 53–83, Blackwell

68 Karmiloff-Smith, A. (1992) *Beyond Modularity: A Developmental Perspective on Cognitive Science*, MIT Press

69 Hindmarch, I. (1973) Eye movements and the perception of phenomenal causality. *Psychologica Belgica* 13, 17–23

70 Shiffrin, R. and Schneider, W. (1977) Controlled and automatic human information processing: II. Perceptual learning, automatic attending, and a general theory. *Psychol. Rev.* 84, 127–190

71 Leslie, A.M. (1986) Getting development off the ground. In *Modularity and the Infant's Perception of Causality* (Geert, P., ed.), pp. 406–437, North Holland

72 Schlottmann, A. and Shanks, D. (1992) Evidence for a distinction between judged and perceived causality. *Q. J. Exp. Psychol.* 44, 321–342

73 Schlottmann, A. (1999) Seeing it happen and knowing how it works: how children understand the relation between perceptual causality and underlying mechanism. *Dev. Psychol.* 35, 303–317

74 Weir, S. (1978) The perception of motion: Michotte revisited. *Perception* 7, 247–260

75 Cavanagh, P. *et al.* Attention-based visual routines: sprites. *Cognition* (in press)

76 Scholl, B.J. and Leslie, A.M. (1999) Explaining the infant's object concept: beyond the perception/cognition dichotomy. In *What is Cognitive Science?* (Lepore, E. and Pylyshyn, Z., eds), pp. 26–73, Blackwell

77 Leslie, A.M. *et al.* (1998) Indexing and the object concept: developing 'what' and 'where' systems. *Trends Cognit. Sci.* 2, 10–18

78 Hauser, M. (1998) A non-human primate's expectations about object motion and destination: the importance of self-propelled movement and animacy. *Dev. Sci.* 1, 31–38

79 Kummer, H. (1995) Causal knowledge in animals. In *Causal Cognition: A Multidisciplinary Debate* (Sperber, D. *et al.*, eds), pp. 26–36, Clarendon Press

Imprinted genes, cognition and behaviour

Anthony R. Isles and Lawrence S. Wilkinson

The idea that genes can influence behavioural predispositions and their underlying psychological determinants is becoming increasingly tractable. In this article, recent findings are reviewed on a special type of inheritance, related to the transmission of traits via what have been termed 'imprinted' genes. In imprinted genes one allele is silenced according to its parental origin. This results in the inheritance of traits down the maternal or paternal line, in contrast to the more frequent mode of inheritance that is indifferent to the parental origin of the allele. Drawing on the advances made possible by combining the approaches of cognitive neuropsychology, behavioural neuroscience and contemporary molecular genetics, the detailed evidence for imprinted effects on behavioural and cognitive phenotypes is considered, focusing on findings from mental disorders, Turner's syndrome and experimental work in animal models. As prevailing evolutionary theories stress an essential antagonistic role of imprinted effects, these data might link such apparently diverse issues as neurodevelopment and the vulnerability to mental disease with the 'battle of the sexes', as joined at the level of cognitive and behavioural functioning.

Genomic imprinting refers to the silencing of one allele of a gene according to its parental origin[1]. The cellular mechanisms underlying genomic imprinting are not completely understood but it is known that the 'imprint mark' occurs during gametogenesis (the production of the sperm or egg) and involves a parent-specific molecular tagging of one of the alleles (Box 1). In the progeny, this leads to a selective silencing of an allele that depends on its parental origin, which in turn, results in the parent-specific monoallelic expression of the trait associated with that imprinted locus. The upshot of these complex molecular events is a form of inheritance that passes on traits down the maternal or paternal line, via maternal or paternally expressed genes, in contrast to the more-frequent biallelic inheritance of traits that is indifferent to the parental origin of the allele.

One pervasive, though not exclusive[2], argument has it that the evolutionary fire driving such a mode of inheritance is related to conflict between the sexes that arises as a result of sexual (as opposed to asexual) reproduction. That is, to put it simply, while males and females need each other to effect

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