

## Primer Culture

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If you are not sure what ‘culture’ means, you are not alone. In 1952, anthropologists Kroeber and Kluckhohn identified 164 definitions of culture and there has been growth rather than rationalisation in the ensuing 70 years. In everyday English, culture is the knowledge and behaviour that characterises a particular group of people. Under this umbrella definition, culture was for many decades the exclusive province of the humanities and social sciences, where anthropologists, historians, linguists, sociologists and other scholars studied and compared the language, arts, cuisine, and social habits of particular human groups. Of course, that important work continues, but since the 1980s culture has also been a major focus of enquiry in the natural sciences.

The founding of the *Cultural Evolution Society* in 2015 revealed that there are now thousands of biologists worldwide investigating the evolutionary origins of culture and trying to explain cultural change using mathematical techniques from population genetics. These biologists are asking when and where in the animal kingdom culture has originated; exploring the behavioural, cognitive, ecological and social factors that make culture possible; and trying to understand how cultural change has interacted with genetic change to produce the rich diversity of human societies. Cultural evolutionists do not always use the term ‘culture’ in a way that ordinary speakers of English would recognise, and, as we shall see, they have developed definitions of culture that relate to their explanatory projects in subtle and interesting ways.

### Culture<sup>1</sup> to Culture<sup>3</sup>

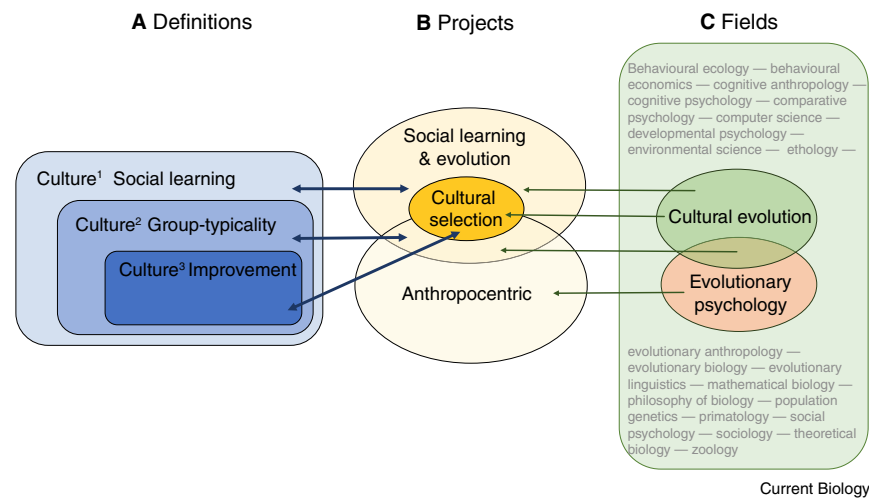
In contemporary research with an evolutionary flavour, just three uses of ‘culture’ are common (Figure 1A), and they all link it with social learning — learning assisted by observation of, or interaction with, another agent or its products. In order of increasing specificity, the term ‘culture’ is used by evolutionists to refer to: first, information

or behaviour acquired through social learning; second, one or more socially learned behaviours shared by the members of a group; or third, socially learned behaviours that are shared by members of a group and have improved over successive episodes of social learning.

It is important not to confuse the first of these definitions, Culture<sup>1</sup>, with the second and third, Culture<sup>2</sup> and Culture<sup>3</sup>, because they represent very different explanatory projects (Figure 1B). The first definition suggests that culture is present in all the many vertebrate and invertebrate animals that are capable of social learning. Grouse have Culture<sup>1</sup> because the females prefer to mate with males with whom they have seen other females mating, and snails have Culture<sup>1</sup> because they sometimes find prey by following the slime trails of other snails. The scope of this minimal definition of culture is yet broader when it is used by those interested in *niche*

*construction* — processes whereby organisms change their environments. Within the niche construction framework, social learning can occur, not only when an animal observes another agent or its recent secretions, but whenever an animal encounters a feature of its environment that has been changed — deliberately or inadvertently, recently or long ago — by other animals. Culture<sup>1</sup> is used when the purpose of enquiry is to find out how social learning influences evolutionary dynamics across the animal kingdom; when asking how social learning contributes to behavioural adaptation, interacts with genetic processes, and semi-detaches animals from ecological constraints. Culture<sup>1</sup> has very little to do with what most people, in science and on the street, think of as culture.

The second definition is more restrictive and closer to what we mean when we talk about human culture in everyday life. To count as Culture<sup>2</sup>, or a



**Figure 1. Logical geography of research on cultural evolution.**

(A) Definitions. The three commonly-used definitions of culture are nested; Culture<sup>1</sup> is more inclusive than Culture<sup>2</sup>, and Culture<sup>2</sup> is more inclusive than Culture<sup>3</sup>. (B) Projects. The three definitions of culture are linked with different explanatory projects. The anthropocentric project, which seeks to understand what makes human lives distinctive, overlaps with the project examining interactions between social learning and evolution. The search for cultural selection (also known as the ‘third-way project’) is part of the effort to understand relations between social learning and evolution, and is sometimes (but not always) part of the anthropocentric project. (C) Fields. People who study ‘cultural evolution’ come from many fields of science (the list here, from behavioural ecology to zoology, is not exhaustive). Each study of cultural evolution relates to one or more of the three explanatory projects. The anthropocentric project is also a focus of evolutionary psychology. Cultural evolutionary research is like evolutionary psychology to the extent that it explains distinctively human behaviour with reference to complex, genetically inherited cognitive processes. Panels A, B and C represent conceptual relations, not volumes of research. For example, cultural evolution and evolutionary psychology are represented by ovals of equal size, but this does not indicate the two fields are yielding similar volumes of research. Similarly, the degree of overlap between the two fields is not an estimate of how many studies of cultural evolution share assumptions with evolutionary psychology.



‘tradition’, a behaviour must be not only socially learned (sufficient for Culture<sup>1</sup>), but group-typical. It must be present in all or many members of one or a few social groups, and absent or rare in other social groups of the same species. And, crucially, the group-typicality must be due to the social learning, rather than to ecological or genetic differences between groups. For example, some groups of rats living on the banks of the Po River eat molluscs, and other groups in the same area of Italy do not. Mollusc-eating would be an example of Culture<sup>2</sup> if the variation between groups arose because, in some groups but not others, lucky or inventive rats had discovered how to dive for molluscs, and passed on this handy trick to other members of their groups through social learning. In fact, Bennett Galef’s research suggests that the group-typicality of mollusc-eating is due to ecological variation; the groups of rats that dive for molluscs live in areas where there are few alternative sources of food. Therefore, it is likely that mollusc-eating in rats is driven by hunger, rather than enabled by social learning, and consequently that it does not amount to Culture<sup>2</sup>.

There is evidence of Culture<sup>2</sup> in primates and other mammals (for example, dolphins, meerkats, mongoose, whales), fish and birds. Some groups of chimpanzees use tools — to hunt invertebrates, crack nuts, or obtain water — which are not used by other groups of chimpanzees. Coral reef fish socially learn where to mate, and local populations use distinct mating sites over generations. New Caledonian crows show regional variation in the construction of leaf tools used to spear and hook grubs, and, in the most rigorous and extensive research on Culture<sup>2</sup>, songbirds have been found to develop distinct regional dialects through social learning. In most species, there is evidence of Culture<sup>2</sup> relating to just one behaviour — for example, mating site selection, leaf-tool making or song dialect — but field studies, where there is limited potential to control for ecological variation, suggest that some groups of great apes have multiple traditions. For example, Carel van Schaik and colleagues have identified more than 20 behaviours — including ‘kiss-squeak’ gestures and creative uses of leaves — that vary across groups of orangutans in Borneo and Sumatra.

Culture<sup>2</sup> tends to be used when the purpose of enquiry is to find out about the origins of human culture. Like users of Culture<sup>1</sup>, researchers who define culture as socially learned group-typical behaviour may have a broad interest in the evolutionary consequences of social learning. However, the primary function of Culture<sup>2</sup>, as a scientific instrument, is to identify behaviour in nonhuman animals that may illuminate the phylogenetic and ecological, social and cognitive factors that have produced the rich potential for group-typical behaviour, belief and technology found in our species.

I shall turn now to Culture<sup>3</sup>. The terms ‘cumulative culture’ and ‘cumulative cultural evolution’, which are used interchangeably, have become increasingly prominent since the 1990s. These terms suggest that social learning can not only produce behavioural variation between groups (Culture<sup>2</sup>) but improve behaviour over generations. You learn a certain knot from me, you discover an even better way of tying that knot, and the agents who learn from you inherit your improved method. More formally, Alex Mesoudi and Alex Thornton recently listed four minimum requirements for cumulative culture or, as I am calling it, Culture<sup>3</sup>: “(i) a change in behaviour (or product of behaviour, such as an artefact), typically due to asocial learning, followed by (ii) the transfer via social learning of that novel or modified behaviour to other individuals or groups, where (iii) the learned behaviour causes an improvement in performance, which is a proxy of genetic and/or cultural fitness, with (iv) the previous three steps repeated in a manner that generates sequential improvement over time” (Mesoudi and Thornton, 2018, p.2).

Some cultural evolutionists, such as Claudio Tennie, believe that Culture<sup>3</sup> is uniquely human, while others argue that the regional variation in tool-use behaviour of great apes and corvids (see above) meets Mesoudi and Thornton’s criteria. Some of the most striking experimental evidence of cumulative culture comes from work on pigeons. Takao Sasaki and Dora Biro found that homing pigeons can improve their skills by flying with a more experienced bird, and when they are put in transmission chains — where, after each novice has become an expert, it is paired with a new, naïve

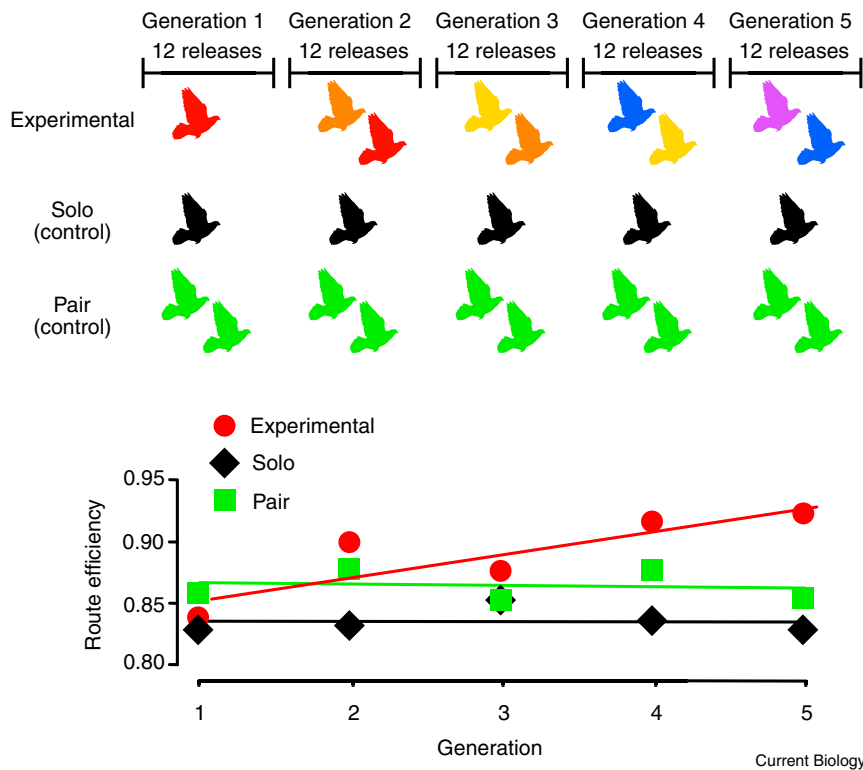
bird — homing performance improves over re-pairing generations (Figure 2).

### The anthropocentric and cultural selection projects

Two subtly different explanatory projects motivate research on cumulative culture or Culture<sup>3</sup>. One of them, the anthropocentric project, also inspires research using Culture<sup>2</sup>. This project aims to explain notable human achievements — from the control of fire and the construction of kayaks, through knowledge of quantum physics to exploration of Mars — and to identify forerunners of the relevant capacities in other animals. Some researchers pursuing this anthropocentric project, often identified as *evolutionary psychologists*, ascribe impressive human achievements primarily to the brilliance of individual human minds (Figure 1C). They acknowledge that we pool our skills and discoveries, but see the features of individual minds, rather than the interaction of minds, as the secret of our success. In contrast, many cultural evolutionists — those interested in Culture<sup>2</sup> and Culture<sup>3</sup> — believe that our achievements are fundamentally collective; we have been able to thrive in a wide range of environments, and to make radical changes to those environments, primarily because we work together, learning from one another.

The other explanatory project, the cultural selection project, relates specifically to Culture<sup>3</sup>, to cumulative culture. This project, also pursued by people who identify as cultural evolutionists, asks whether Darwinian selection occurs in the cultural domain, whether ‘cultural selection’ occurs in any species. Specifically, it asks whether behavioural adaptation at the population level can occur via a process in which variants are generated by mistake or trial-and-error learning rather than mutation, and inherited through social interaction rather than genetic mechanisms, and where selection depends on the bearer’s success in passing on their variant to biological offspring and to unrelated individuals via social learning — to ‘babies’ and to ‘students’.

The cultural selection project is also known as the ‘third way project’ because two routes to population-level behavioural adaptation are already well-known. First, in human and nonhuman animals, the fit between a population’s



**Figure 2. Culture<sup>3</sup> in pigeons.**

Upper panel: In each chain of the experimental group, a single pigeon (red) was first released from the same site 12 times, then partnered with a naïve bird (orange) and flown as a pair a further 12 times. The first bird was then replaced by a third bird (yellow) and this new pair (orange–yellow) was released 12 times. This procedure was repeated until the fifth-generation naïve bird (purple) was added and flown a final 12 times. In the control groups, single pigeons (Solo) and fixed pairs (Pair) were released the same number of times as the experimental group (60 flights). Lower panel: Linear mixed-effects model fitted to the final flights of each generation for all three treatment groups. Over generations, route efficiency continued to increase in the Experimental group but quickly plateaued in the Solo and Pair groups. (Data from Sasaki and Biro, 2017.)

behaviour and the environment in which it occurs can be enhanced by genetic evolution. For example, natural selection acting on genetic variants is the primary architect of web-spinning in spiders. Second, at least in humans, the fit can also be improved by what Daniel Dennett calls ‘intelligent design’ — by the foresight and planning of individuals and groups. Intelligent design is what many evolutionary psychologists take to be of overriding importance. For example, confronted with the threat of COVID-19, governments across the globe anticipated what its effects would be, planned methods of mitigating the effects using scientific evidence, and attempted to change people’s behaviour by implementing those plans via a range of institutions. The cultural selection, or third way, project asks whether there is *another* way in which the behaviour

of a population can become adapted: a process that, in contrast with genetic evolution (the first way), selects among socially learned rather than genetically inherited variants, and, in contrast with intelligent design (the second way), where the adaptiveness of the selection does not depend on individuals or groups being smart enough to design novel solutions or to recognize what works and what does not.

**Foresighted and short-sighted cognition**

The anthropocentric and cultural selection projects can be difficult to tell apart. Many cultural evolutionists are interested in both projects. Some of these cultural evolutionists get their wires crossed, and others, in an entirely coherent way, see cultural selection as the answer to the anthropocentric

question; as the thing that explains distinctively human achievements. But the differences between the anthropocentric and cultural selection projects, although rarely recognised, are important. Specifically, the anthropocentric project is compatible with the assumption — widely held since the Enlightenment and backed by evolutionary psychology — that humans are able to do remarkable things because each of us is smart. In contrast, the cultural selection project raises a radically new possibility. It suggests that many of our striking achievements, and those of other animals, depend on each of us being pretty dumb; that wisdom comes from the population-level process of cultural selection, rather than the workings of individual minds.

To see how this counter-intuitive idea could be true, imagine a population of animals where two different twig types are used to extract edible grubs from tree trunks — fat and straight twigs (A) or thin and bent twigs (B) — and juveniles socially learn which type to use. The juveniles’ social learning (Mesoudi and Thornton’s second requirement for cumulative culture), and any subsequent improvement (third requirement), could be foresighted or short-sighted. In the foresighted case, each juvenile might decide whether to adopt A or B after careful comparison of the number of grubs procured by models using A and B, and any improvement might be based on deep thought about where the grubs tend to be located within the trees, and the causal powers of different twig types. The foresighted social learner is Rodin’s Thinker.

In the short-sighted case, whether a juvenile adopts A or B might be determined by who she happened to see just before she made her first attempt to secure a grub. If she saw an A-user she selects an A-type twig, and if she saw a B-user she selects a B-type twig. Whether her attention was caught by an A-user or B-user may, in turn, have depended on how many grubs each actor was securing. After all, hungry animals pay close attention to food and therefore see other objects and events in its vicinity. But in the short-sighted scenario, juveniles do not compare the number of grubs produced by A-users and B-users. Their choice of models is determined by what or who grabs their attention rather than clever strategies.

It depends on simple attentional mechanisms found throughout the animal kingdom, not on causal reasoning, planning or metacognition (thinking about thinking).

Similarly, in the short-sighted scenario, if a juvenile improves the socially-learned method — for example adopts B and then begins using twigs bent in, not one, but two places — she does it by trial-and-error. She does not have mental models of the location of the grubs in the tree trunk, or of the causal powers of twigs, she just has a go with a range of twigs that are similar to the B-type — the type she learned from her model — and settles on the variant that works best for her. If the foresighted learner is Rodin's Thinker, the short-sighted learner is Wash 'n' Go.

Now, for the anthropocentric project it does not matter much whether the requirements for cumulative culture are met through foresighted or short-sighted cognitive processes. In either case, the resulting improvement can be chalked up as an instance of the collective intelligence that makes humans special, or as an evolutionary precursor of that 'specialness'. If the processes are foresighted, the cultural evolutionists' view is similar to that of evolutionary psychologists — the intelligence of individuals is crucially important — but the cultural evolutionists' perspective is still distinguishable from a standard evolutionary psychological view to the extent that it emphasises the importance of social learning (Figure 1C). In contrast, for the cultural selection project, the difference between foresighted and short-sighted processes is crucial. Insofar as the requirements for cumulative culture are met by foresighted cognitive processes, they indicate not cultural selection (the third way) but intelligent design (the second way).

If cumulative culture is critically dependent on foresight, a version of the Enlightenment view of humanity is vindicated. The secret of our success lies in the intelligence of individuals, on each of us being Rodin's Thinker, even if that intelligence requires networks of minds, across time, to meet its full potential. The alternative — dependence of cumulative culture on short-sighted cognitive processes — would support a much more radical view. It would suggest that some of the most

impressive achievements of humans, and other animals, depend on individuals being dumb rather than smart — willing to copy the behaviour of others in Wash 'n' Go style, with minimal assessment of the behaviour's utility.

### Fruits rather than seeds

The cultural selection project raises the possibility that complex cognitive processes are fruits rather than seeds of culture. In the past it has been widely assumed that Culture<sup>2</sup> and Culture<sup>3</sup> require social learning based on fancy, foresighted cognitive processes — for example, a capacity to copy the fine details of body movements ('imitation'), to understand models' intentions ('theory of mind' or 'shared intentionality'), and to weigh up the pros and cons of copying one model rather than another ('social learning strategies'). In other words, it was assumed that complex cognitive processes are the seeds of culture; once they have evolved in a lineage, via genetic inheritance, there is the potential for significant regional variation in behaviour (Culture<sup>2</sup>) and for improvement of socially learned traits over generations (Culture<sup>3</sup>). The cultural selection project makes clear that this need not be the case. Cultural selection could produce Culture<sup>2</sup> and Culture<sup>3</sup> without complex cognition. Adaptation via cultural selection, like adaptation via genetic selection, requires offspring to be similar to their parents, and a tendency for more effective variants to be copied more often than less effective variants, but it does not require these conditions to be met via complex forms of social learning.

Apart from their homing skills, pigeons do not seem to be especially smart. Therefore, cumulative culture in pigeons (Figure 2) provides a proof of principle that Culture<sup>3</sup> can get off the ground without the involvement of complex cognition such as imitation, theory of mind, and strategic thinking. Further evidence comes from the dolphins of Shark Bay, Western Australia, where there are signs that a sponge-based foraging technique, learned in a cognitively undemanding way by juveniles from their mothers, is evolving via cultural selection.

So, if complex cognitive processes are not the seeds of culture, is it just a coincidence that humans are both smart and heaving with culture? Do our capacities for imitation, theory of mind

and other complex cognitive processes have nothing to do with our outstanding diversity (Culture<sup>2</sup>) and propensity to improve socially learned behaviour over generations (Culture<sup>3</sup>)? That seems very unlikely, but an alternative solution to the puzzle is emerging: Recent research on the childhood development of imitation, theory of mind, and other complex cognitive processes suggests that — like beliefs, preferences, technologies and social conventions — these cognitive processes are products of culture; fruits rather than seeds of cultural selection. For example, recent studies have shown that newborn humans cannot imitate; imitation is not 'in our genes'. Instead, the cognitive mechanism enabling imitation is built in the course of childhood through social interaction with parents and other expert imitators, and, at the population level, the imitation mechanism was shaped to do its job by cultural selection; it is a product of culture–culture coevolution.

But if this is true of imitation and other distinctively human cognitive mechanisms, if they are fruits rather than seeds, then what are the seeds? What determines whether a lineage, capable of generic but not fancy social learning, develops group-typical behaviour (Culture<sup>2</sup>) or cumulative culture (Culture<sup>3</sup>)? Modelling of archaeological and anthropological data, and studies of nonhuman primates, suggest the answer is social factors. Rather than cognitive factors, the social structure of a species (for example, how long juveniles spend in close proximity to their parents), and demographic variables (for example, the size of social groups and their spatial distribution) have a major influence on the probability that Culture<sup>2</sup> and Culture<sup>3</sup> will emerge. For example, it is possible that cultural selection of knowledge and skills can get started only in species where young learn almost exclusively from their parents and cultural fitness depends on biological reproduction. Similarly, it is possible that cultural selection of knowledge and skills can only take off — become so important that it supports the cultural selection of complex, specialised cognitive mechanisms — when populations are so large that there is minimal risk of experts being wiped out by epidemics, conflict, and climatic events.

**Conclusion**

Culture has inflated. In the time frame of Kroeber and Kluckhohn's work, 70 years ago, the idea that culture can be equated with social learning (Culture<sup>1</sup>) is relatively new, and socially learned group-typical behaviours (Culture<sup>2</sup>) used to be called 'traditions' rather than culture. Consequently, increasing use of the term 'cumulative culture' (Culture<sup>3</sup>), along with Mesoudi and Thornton's heroic efforts to define it, are attempts to protect two significant explanatory projects: to work out what makes human lives so unusual (the anthropocentric project), and to find out whether Darwinian evolution occurs in the cultural domain (the cultural selection project). Recent research with these aims suggests that social rather than cognitive factors play a dominant role in the emergence of cumulative culture. We humans are smart because we are cultured, rather than cultured because we are smart.

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**Correspondence****Separation in the visual field has divergent effects on discriminating the speed and the direction of motion**

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Local motion in a visual scene allows the detection of prey or predator and predicts their future positions. Relative motion segregates objects and reveals their 3D relationships. 'Optic flow' — the motion of texture across the field — guides locomotion and balance. Given these several uses of visually perceived motion, it is unsurprising that many species have evolved hard-wired neural mechanisms to extract motion as a primitive feature of the visual world [1]. In the cortex (e.g. [2–4]), and even the retina [5], of primates, cells are found that respond selectively according to direction of motion. In visual areas V1 and MT, some directionally selective cells are also tuned for the second attribute of motion, speed [3]. It might be thought that the brain derives a single velocity signal from the activity in this population of neurons — since speed and direction must often be combined to predict an object's future position or to derive a 3D structure. However, we report here a striking difference in discrimination of the two attributes: Thresholds for direction, but not those for speed, increase with the spatial separation of the stimuli.

Several previous findings hint that direction and speed may be differently computed. For example, direction discrimination is poorer for oblique than for cardinal directions, but this is not the case for speed [6]. Also, speed discrimination for arrays of random dots is of similar precision whether the two arrays move in the same, in opposite or in orthogonal directions [7]. And transcranial magnetic stimulation, applied medially, is reported to impair speed discrimination disproportionately relative to direction discrimination, under conditions where the physical

stimuli and their discriminability were similar [8]. In the present experiment, we asked how the precision of discriminating speed or direction changed as the spatial separation of the discriminanda increased. The stimuli were pseudo-random arrays of moving dots, briefly presented (Figure 1A). They fell on an imaginary circle (radius: 5 degrees of visual angle) centred on the fixation point [7]. The spatial separation of the two arrays varied between blocks and had a maximal value of 10 degrees of visual angle, while their eccentricity remained constant.

In alternating runs, we measured the discrimination of the two attributes. In both cases, the participant's task was chosen to be the simplest possible: detection of the presence of a difference. In one of two intervals (Figure 1B), the two arrays moved in the same direction and at the same speed; in the other, they differed in speed or in direction according to the condition tested. An adaptive procedure estimated the stimulus difference that supported 79.4% correct (see experimental procedures in Supplemental Information, published with this article online). The reference speed at which discrimination was measured was 5 deg.s<sup>-1</sup> and the reference direction was 135° from vertical (4.30 o'clock).

Normalised average thresholds for 10 participants are shown in Figure 1C as a function of the spatial separation of the two arrays of moving dots. A striking difference is seen between the results for discrimination of direction and for discrimination of speed. Thresholds for detecting a difference in *direction* (open circles) increase systematically with the spatial separation of the two arrays (One-way Repeated Measures ANOVA (after Greenhouse-Geisser correction):  $F(2.739,24.652) = 18.44, p < 0.001$ ). In contrast, thresholds for *speed* (closed circles) vary little with separation, a result we previously found for discrimination of spatial frequency. In fact, a one-way Repeated Measures ANOVA with Greenhouse-Geisser correction does show a marginally significant effect of separation ( $F(3.181,28.628) = 3.414, p = 0.029$ ), owing probably to the *higher* thresholds for abutting arrays. The latter effect

