How the brain creates culture

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Abstract (English & German)
It is characteristic of human culture that we learn about the nature of the world from our predecessors and pass such knowledge on to our descendants. However, learning about the world from observing the behaviour of others is widespread throughout the animal kingdom. There are two features of human interactions that are critical for the development of the cumulative culture that is uniquely human. First, there is the largely automatic and unconscious process by which humans mimic each other, generating alignment of behaviour and cognitive processes, which enhance group-oriented behaviour. Second, there is the deliberate and conscious process, which allows humans to discuss with each other the nature of the world and how the mind works. Such discussions have top-down effects on behaviour and experience. These effects can result in cultural consensus on topics such as how actions are controlled, leading to ideas about responsibility for action which are critical for social cohesion. It is this uniquely human ability, to reflect and report on our experiences, which enables the development of cumulative culture. There is preliminary evidence that this metacognitive ability depends upon the anterior frontal cortex (Brodmann area 10), one of the most recently evolved regions of the human brain. However, brain plasticity is such that the acquisition of the various new skills emanating from cumulative culture will, in their turn, influence the development and functioning of the human brain.
1.0 Learning about the world from others

Without culture each of us would have to learn afresh about the world. This would be hard work and inevitably we would make many mistakes that could be disastrous. We can avoid these problems by learning about the world from others; parents, teachers, wise elders, and peers with somewhat different experiences to our own. Books and institutions are also rich sources of information about the world which we can rely on to guide our individual journeys into the unknown. In addition, through novel individual experiences, the information in these sources is continuously being updated and expanded. This is the ‘ratchet effect’ (Tomasetto 2009a) that creates cumulative culture. Cumulative culture is unique to humans. In the course of evolution some ability, instantiated in the human brain, has emerged that has enabled us to create cumulative culture. In this essay I will review recent evidence from the fast developing discipline of social cognitive neuroscience that provides pointers to the cognitive and neural mechanisms that enable cumulative culture to emerge.

1.1 Learning from observation

A plausible hypothesis is that culture emerges through an ability to imitate and learn from others. By following others and by observing their choices it is possible to learn, not only about places, but also about objects, actions, and other agents. Human and other animals can learn a lot from simply observing others even when this behaviour has no deliberate communicative intent, and when social information is being used just like any other publically available information in the environment (Danchin et al. 2004).

Learning about places. Fish are among the many animals that learn about the location of food by observing the behaviour of others. An individual, isolated fish (here the nine-spined stickleback) may have learned that food can be found on the left side of a tank (private information) and will therefore swim to the left when given the choice. But, after a delay of 7 days, if other fish can be observed feeding on the right side of the tank (public information), then the individual will swim to the right (Van Bergen et al. 2004). This is presumably because the private information about food being on the left is too old and unreliable. Examples of social influence on
foraging behaviour can be observed in many other animals (Galef and Girardeau 2001), including humans. The phenomenon is certainly well understood by restaurateurs, who seat early arrivals in the window to attract more customers. People prefer to go to places where other people go (Rieua and Girardeau 2011).

A related process is gaze-following through which we automatically look at the place towards which someone else is looking. This example of social influence has been demonstrated in ravens, goats, dogs and primates, including lemurs (Shepherd and Platt 2008; reviewed in Zuberbühler 2008). Gaze-following is reliably used by human infants to learn about objects and events from around 1 year of age (Carpenter et al. 1998; Flom and Johnson 2011).

1.1.1 Learning about objects. Animals need to distinguish between nice objects that should be approached and dangerous objects that should be avoided. Such information can also be acquired through observation. For example, Mineka and colleagues (1993; 1984) have demonstrated that rhesus monkeys acquire a fear of snakes very quickly by observing another monkey showing fear towards a snake. Fear conditioning through observation has also been demonstrated in humans (Olsson et al. 2007). But learning about objects is not just restricted to fear conditioning. For example, objects looked at by other people are preferred more than objects that do not receive attention (Bayliss et al. 2006).

1.1.2 Learning about actions. Many animals learn which actions to perform by observing others (Huber et al. 2009). For example, chimpanzees will imitate a demonstrated sequence of actions to gain access to food in a puzzle box (Whiten 1998). Wild mongoose pups learned, merely by observing an adult, to open Kinder-eggs by either smashing them on the ground or biting them (Müller and Cant 2010). Such imitative learning can also be seen in human infants from around the age of 1 year (e.g. Carpenter et al. 1998).

1.1.3 Learning about agents. Learning about other individuals and how to interact with them is vital for all social animals. This is especially relevant for mate choice. Naïve female fruit flies will choose as partners male flies they have seen mating with
experienced females (Mery et al. 2009). Effects of observation on mate choice are also observed in guppies and quail (White 2004). Learning about the status of conspecifics is also important for knowing whom to approach and whom to avoid. Many animals can infer social rank by observation alone. For instance, fish learn whom not to pick a fight with through observation (Groenick et al. 2007).

1.1.3 The advantages of learning by observation. How important is this form of learning in comparison to non-social alternatives such as trial-and-error learning? Laland and colleagues (Rendell et al. 2010) instigated a computer tournament in which participants proposed strategies for combining learning by observation (copying) with learning by direct experience (trial-and-error) in order to acquire adaptive behaviour in a complex environment. The most successful results were obtained by strategies that relied heavily on copying. Indeed, the most successful strategy relied almost exclusively on this and demonstrates the power of learning by observation over learning from experience.

Why was copying so successful in this context? Two reasons seem likely. First, as I already mentioned, the observer avoids having to make errors that are an essential part of trial-and-error learning. But, in addition, because demonstrators will selectively perform the actions that they have found to be most beneficial for themselves, they effectively and inadvertently act as a filter to provide the information that is most useful for an observer. Copying is a highly adaptive means of gaining knowledge (Rendell et al. 2010).

2.0 Learning to be part of a group
Learning from observing others can be found throughout the animal kingdom (Galef and Laland 2005; Heyes and Galef 1996; Leadbeater and Chittka 2007). This is not a phenomenon that is unique to humans. It is not sufficient for the emergence of cumulative culture.

Is there something qualitatively different about the way humans learn by observation? Learning by observation creates a form of imitation. We go where others go and do what others do. However, imitation can occur at different levels
and can have different functions. Both of these variations can be observed in the phenomenon of over-imitation. The kinds of imitation I have discussed so far have been concerned with the goal of learning about the world. More specifically the goal is to obtain a resource such as food, and, by imitating others, we learn the action needed to achieve that goal. This is not the case with over-imitation.

2.1 Over-imitation
Children and chimpanzees have been studied when they learn, by observation, how to open a puzzle box to get a reward. For example, to open the box the demonstrator might use a wand to push out a red wooden bolt, which is then used to tap the empty upper compartment. The demonstrator then pulls out the round plug in the centre of the door assembly and uses the wand to retrieve the reward. The first part of this procedure is irrelevant for getting to the reward and can easily be seen to be irrelevant. Nevertheless, children of three to five years persist in imitating the irrelevant actions (over-imitation). Furthermore, the children persist even in situations when there are competing tasks demands and even in the face of direct warnings (Lyons et al. 2011; Lyons et al. 2007). In other words, they persist in strict imitation even when this is against their individual interests. Chimpanzees are much less likely to imitate the irrelevant components of the action and go to the reward as quickly as possible (Horner and Whiten 2005). In humans, the copying of the irrelevant actions actually increases with age, so that adults perform the task with even more emphasis on conformity with the irrelevant actions than children (McGuigan et al. 2010).

2.2 Emulation and mimicry
Over-imitation is an example of process-oriented imitation (Tennie 2009), also referred to as mimicry (Hamilton 2008). This kind of imitation can be contrasted with product-orientated imitation, or emulation. An action is emulated when the same goal is achieved by actor and observer. For example, if an adult picked up a book with one hand, a child, lacking sufficient strength, might use two hands when imitating the action. The same goal is achieved, but the actions are not identical. Mimicry, in contrast, requires that the kinematics of the movement be copied as accurately as possible. Mimicry is especially important for imitating intransitive
actions, that is actions, such as expressive gestures, which are not directed towards an object. Mimicry is a form of imitation that is strongly developed in humans, but lacking in monkeys (Visalberghi and Fragaszy 2002) and only seen in very limited circumstances in apes (Tennie et al. 2009). Emulation, on the other hand is frequently observed in monkeys and apes. Over-imitation involves mimicry since the way the action is performed is at least as important to imitate as the goal of the action.

This faithful copying of actions, which overrides getting a primary reward by other means, is a striking feature of human culture. It is the basis of the rituals that enhance group cohesion (Durkheim 1912) and also provides a means for creating distinct group identities. As William McDougall (1926 page 352) wrote: “Most Englishmen would scorn to kiss and embrace one another or to gesticulate freely, if only because Frenchmen do these things”.

2.3 Neural mechanisms for imitation
An obvious candidate for a mechanism for imitation in the brain is the mirror neuron system (Rizzolatti and Craighero 2004) where neurons can be found which become active during both the observation and the execution of actions. The two major components of this system are the inferior frontal gyrus (IFG) and the inferior parietal lobule (IPL). Closely associated also is a region stretching from the lateral occipital sulcus to the superior temporal sulcus which is activated by action observation and probably provides the visual input to the mirror neuron system. However, we need an account of imitation that distinguishes between emulation and mimicry.

In a series of studies, Hamilton and her colleagues (reviewed in Hamilton 2008) provide evidence of for a dual route account of action imitation. These studies took advantage of the phenomenon of repetition suppression in fMRI, a technique that provides a more precise estimation of the function of populations of neurons than the more traditional subtraction method (Grill-Spector et al. 2006). Observation of the repetition of the same goal (grasping a bottle) rather than a novel goal (e.g. taking a cookie) resulted in suppression of activity in the anterior intraparietal
sulcus (HAMILTON and GRAFTON 2006), a component of the IPL node in the mirror neuron system. In contrast, when the same goal (e.g. grasping a bottle) is achieved by a different kind of grasp (e.g. finger tips or whole hand), suppression to repeated grasps is seen in two other components of the mirror neuron system, inferior frontal gyrus and the occipito-temporal region (HAMILTON and GRAFTON 2007). These results suggest first, that the parietal node of the mirror system represents the goals of actions; second, that the occipito-temporal node represents the visual kinematics of actions; and third, that the inferior frontal gyrus represents the motor kinematics of actions. Emulation requires an indirect route via parietal cortex, where goals are represented. Mimicry, in contrast, involves a direct route from visual analysis to motor execution¹.

2.4 Social modulation of mimicry
The function of this kind of imitation is not about learning to achieve a goal. It is about learning ‘the way we do things’ in order to become part of the group. As a result the tendency to mimic is strongly influenced by social factors. One example is provided by the effect of being excluded by your in-group. After such exclusion, both adults (LAKIN et al. 2008) and children (OVER and CARPENTER 2009) increase the extent to which they imitate the actions of a confederate, but only if this confederate is a member of the in-group.

Mimicry also differs from emulation in the extent that it is modified by social cues. For example, direct eye contact specifically enhances mimicry of hand actions (WANG et al. 2011) and also emotional expressions (BAVELAS et al. 1986).

2.5 Mimicry and alignment
In addition to creating group cohesion, mimicry can also aid communication. This form of mimicry is referred to as alignment. During verbal discourse the linguistic practices of the people involved become aligned at many levels (PICKERING and GARROD 2004), by using similar words, similar speech rates and similar postures (CHARTRAND and BARGH 1999). This alignment assists comprehension. For example, participants who imitated the accent of a speaker improved their comprehension of that speaker (ADANK et al. 2010).
When interacting with others alignment involves, not only the imitation of motor actions, but also the ‘imitation’ of more abstract entities, such as goals, knowledge and beliefs. That this alignment occurs automatically is revealed by interference effects on performance, such as increases in reaction time. For example, Sebanz and her colleagues (2003) have shown that people automatically take account of the goals of the person they are working with. In a seminal study these authors capitalized on spatial compatibility effects in reaction-time tasks (the Simon effect). The imperative signal was colour: press the left button for a red stimulus and the right button for a green stimulus. However, the stimuli also varied in spatial location, which could be either congruent or incongruent with the required response. Thus, the response was congruent when the red stimulus was left oriented and incongruent when the red stimulus was right oriented. When the task was performed by a single individual as a two-choice reaction time task, there was a strong effect of congruence, that is, congruent responses were made faster than incongruent ones. When, however, the task was performed as a go/no-go task, so that the participant had only to press the left button to red stimuli, the congruency effect disappeared. The innovative condition involved bringing in a second participant to perform the other half of the go/no-go task, i.e. to press the right button to the green stimulus. In this context, even though the original participant was still performing the identical one-choice, go/no-go task, the congruency effect returned and spatially incongruent responses were slowed. This effect depends upon the social relationship between the two people involved (Hommel et al. 2009).

When performing a task alongside someone else, we cannot help but take account of the stimulus–response requirements of the task the other person is doing.

Similar interference effects can also occur through automatically representing the knowledge of others. In the studies of Samson and her colleagues (Qureshi et al. 2010; Samson et al. 2010) differences in the knowledge of two people were created through their seeing the same scene from different viewpoints. Thus, one viewer might be able to see two black disks, while the other viewer can only see one of them, since the other is behind her. Many studies have demonstrated an effect of such incongruence (see Samson et al. 2010 for a review). For example, participants
take longer to report what another can see (e.g. number of black disks), if it is different from what they can see. However, there is also a detrimental effect even when there is no requirement to take account of the other person’s viewpoint. Participants were never asked how many black disks the other person could see, but only how many they could see. Nevertheless, the mere presence of another person in the room with different knowledge slowed down this response. This result shows that we cannot help taking account of the knowledge of others when it is different from our own.

Finally, a recent study shows that we also automatically take into account the beliefs of others, since interference occurs when beliefs are discrepant. Infants of seven months as well as adults were shown a scenario in which a ball went behind a screen (KOVÁCS et al. 2010). Under some conditions, the ball then emerged again and left the scene. Finally, the screen was raised to reveal the ball or an empty space. The infant’s looking time was used as a measure of surprise. If the ball was unexpectedly revealed to be behind the screen, the infants looked longer. Under the critical conditions, another observer, a Smurf, was also present. This observer would be present when the ball went behind the screen, but might be absent when the ball emerged and left the scene. When this observer returned, he would have the false belief that the ball was still behind the screen. The presence of this observer with a false belief influenced the behaviour of the infants. In the presence of a Smurf who falsely believed that the ball was still present, they were not so surprised (in terms of shorter looking time) by the appearance of the ball even though they had seen it leave. The same effect was shown by adult participants, but here, the experimenters used reaction time to report the presence of the ball, rather than looking time. These observations suggest that adults and infants automatically take account of the beliefs of others when these beliefs are different from their own. The effect is not observed in monkeys (MARTIN and SANTOS 2014).

2.6 The we-mode
In the tasks just described, automatically taking account of the knowledge and intentions of others made individual performance worse. However, when we are working together as a team, there will be an advantage for us to take account of our
partners’ goals, knowledge and beliefs. What the results discussed above reveal, I suggest, is that, in the presence of someone with whom we might socially engage, we automatically enter a state, the we-mode, in which our environment and the task in which we are engaged are represented from the point of view of the team rather than the individual (Gallotti and Frith 2013).

In order to interact successfully with the world, we need to restrict our attention to the objects and actions most relevant to our current goals. This can be achieved by representing objects and actions in a saliency map (Koch and Ullman 1985) or value map (Kasderidis and Taylor 2005). In this map, objects relevant to current goals have higher saliency values and more readily elicit attention. However, the value of the objects in the space will be modified by the extent to which actions, such as grasping, can be performed on them. So, for example, objects that are out of reach will have lower saliency (or, in the case of motor acts, affordance) values. The level of affordance is reflected in the amplitude of the motor evoked potentials (measured with trans-cranial magnetic stimulation) elicited by the presentation of an object. These MEPs will be higher when the object is presented within reach (Cardellicchio et al. 2013). However, the presence of another person with whom I could interact, modifies this saliency map. Now the affordance is not only high when it is within my reach. It is also high if it is within reach of this other person, even though it is not within my reach (Cardellicchio et al. 2013). A prediction, yet to be tested, would be that relevant objects that other people could not see would have lower affordance values even though I could see them. This would suggest a mechanism for the results of the studies of Samson’s group discussed above (Samson et al. 2010) showing that we automatically take account of the knowledge of others. The same mechanism could also underlie the biased pooling of information observed by Stasser & Titus (1985). Group discussions are biased towards information that group members already hold in common before discussions begin. The group does not gain full advantage from the pooling of unshared information. I suggest that this phenomenon is caused by the adoption of the we-mode. This biases everyone in the group towards shared information.
The concept of the we-mode was originally formulated to explain why humans seem to be much more cooperative than other primates with regard to sharing resources and showing reciprocal altruism (Moll and Tomasello 2007; Rekers et al. 2011; Tomasello 2009b). Such behaviour can be studied when people play economic games such as the prisoners’ dilemma and the ultimatum game (Jensen et al. 2007). The payoff matrix for the prisoners’ dilemma game is such that a ‘rational’ player should always defect, rather than cooperate, since this response will give a higher payoff what ever the other player does. However, as a group, the players would do better to cooperate. If a player considers only himself (the I-mode), then his choice of how to respond will be dominated by his individual payoff matrix. However, Bacharach (2006) has suggested that players adopt the we-mode. Here their choice is determined by a group payoff matrix, in which cooperation gives the highest payoff. The group affordance map of objects, described above, which promotes joint action, is analogous to the group payoff matrix, which promotes cooperation.

The concept of the we-mode captures the enhanced tendency of humans to form groups marked by cooperation and mental alignment. Such grouping provides a crucial basis for the emergence of cumulative culture. But alignment and cooperation alone are not sufficient.

3.0 Top-down control through instructions: the origin of culture

The various mechanisms I described in the last section are special cases of top-down control in which the social context affects the way stimuli are perceived and actions are performed. In these cases the top-down effects are implicit in the situation. More frequently top-down control is exerted explicitly. For example, every time we instruct our volunteers how to behave in our experiment we are exerting top-down control (Roepstorff and Frith 2004). Such instructions have an immediate impact on brain function. This is illustrated in the contrast between two early brain imaging experiments exploring the perception of colour. In the first experiment volunteers lay in the scanner and passively observed two sets of stimuli, which were identical except that one set contained colour, while the other contained only shades of gray. In comparison with the gray stimuli, the coloured stimuli activated V4, the region in extra-striate visual cortex specialised for colour vision (Zeki et al. 1991). The
participants in this study had minimal instructions. They were simply required to look at the stimuli. In the second experiment, there was only one set of stimuli. Each stimulus contained many small objects, which varied in colour and shape. On some trials participants were instructed to attend to shape, while on other trials they were instructed to attend to colour. Here also there was greater activity in V4 when participants were attending to colour than when they were attending to shape (Corbetta et al. 1991). However, this activity was not directly caused by the stimuli, since these were identical in the two conditions. The instruction, ‘attend to colour’ altered the way the brain processed a stimulus.

3.1 The Bayesian brain
The essence of top-down control, whatever the source of that control, is that the state of the brain, prior to the appearance of the stimulus, influences the way the stimulus is perceived and the action that is taken. This is in contrast to bottom-up control in which perception and action is entirely determined by the stimulus. Outside the laboratory, however, it is very rare for control to be exerted in only one direction. In most situations bottom-up and top-down processes occur together. Such two-way control is best captured within a Bayesian framework (Hohwy 2013). The basic idea is that the main function of the brain is to make predictions in order to choose the behaviour most likely to produce the best outcome in the current circumstances. To make predictions we need to have a model of the world: What is it that we are confronted with, and if there are agents, what are they going to do next? If I believe I am confronted by an elephant, then I can predict what I will see if I move my eyes and also what I will feel if I touch the object (Kersten et al. 2004). Likewise, if I believe that Fred is thirsty, then I predict he will reach for the glass (Kilner et al. 2007). In either case, if my prediction is wrong, then I will alter my belief (perhaps it’s a rhinoceros, perhaps Fred is not thirsty). This mechanism has both top-down and bottom-up components. Top-down there are the prior beliefs or expectations that enable predictions to be made. Bottom-up there is the evidence from the senses that enables the predictions to be tested. Bayes’ theorem (Bayes 1763/1958) indicates the extent to which a prior belief should be altered given new evidence.

3.2 Where do the priors come from?
An important question to ask about such a system is, where do the prior beliefs and expectations come from? One obvious source is past experience (Suppes 2007). For example, when playing tennis against a particular opponent not all shots are equally likely. We might learn that, with this opponent, shots come more frequently towards the left than the right. Optimally combined with the evidence from our senses, this prior belief will give us an advantage. For example, if the visibility is reduced we should put more weight on the prior belief: if in doubt, go to the left (Kording and Wolpert 2004). This kind of learning will happen automatically and without awareness.

There is however, another source of prior beliefs and expectations, and this is probably unique to humans. Just as we can learn from others where to look and what to do, we can also acquire our beliefs and expectations from others. This typically occurs as a result of deliberate communication, such as instruction and gossip. Furthermore, the prior beliefs we acquire from others seem to be given greater weight than the prior beliefs we acquire from direct experience (Delgado et al. 2005; Sommerfeld et al. 2007).
Figure 1: A Bayesian Hierarchy (based on figure 2 in FRISTON 2005). 'Higher' areas deal with more abstract information about the world (e.g. text), while 'lower' areas deal with more concrete data (e.g. letters). The higher area attempts to fit its abstractions to the data it receives from lower areas by sending back to them a reconstruction best fitting the lower level view. The lower area attempts to reconcile the reconstruction of its view that it receives from higher areas with what it knows, sending back the features in its data which are not predicted by the higher area. The diagram illustrates how this hierarchy of mutual constraint can be extended beyond the individual person into the realm of culture. There may well be more levels within the person than are shown in this diagram.

Representation units (right ovals) encode the conditional expectation of causes (i.e. best guesses as to what is causing the sensory input). These expectations are adjusted to minimize the discrepancy between their predicted value and the mismatch incurred by their prediction of the level below. For example, the words units must best match the expectation generated by the text (above) and the evidence provided by the letters (below). The representational units are subject to two, locally available, influences (dotted arrows): a likelihood or recognition term (evidence) mediated by forward connections from the error units (left ovals) at the level below and an empirical prior (belief) conveyed by error units at the same level.

Error units (left ovals) are also subject to two, locally available, influences (solid arrows): a prediction from representation units in the level above and lateral influences from the representational units at the same level. Prediction error is constructed by comparing the activity of representational units within the same level, to their predicted activity conveyed by backward connections.
3.3 The power of instruction and gossip.

When we interact with others it is important for us to learn whom we can trust. This process can be studied though the use of so-called economic games in which participants learn that some of their partners can be trusted to make fair returns of the money invested in them, while other partners are not to be trusted. This learning process is nicely captured through the Bayesian mechanism described above. When we invest money in a partner, on the basis of our degree of trust (the prior belief), we can predict how much of our money will be returned. If this is more than expected (positive feedback), our degree of trust increases, if it is less (negative feedback) our degree of trust decreases. Several studies have shown that activity in the caudate nucleus reflects the nature of such feedback on a trial-by-trial basis (e.g. Delgado et al. 2000).

However, in real life we do not typically interact with complete strangers. We choose as doctors or plumbers people who have been endorsed by a professional body or recommended by a friend (Tennie et al. 2010). Our trust in such people is not determined by direct experience, but by reports from others. Delgado and colleagues (2005) explored this process in the laboratory by providing participants with vignettes about the supposed moral character of the people they would be playing with (e.g. “An English graduate student who had volunteered for inner-city teaching and rescued a friend from a fire during a concert”). This prior information had detectable effects on both behaviour and neural activity. In terms of behaviour, participants showed greater trust (i.e. invested more money) in partners they believed to be of good moral character, even though these partners behaved no differently (in terms of how much money they returned) from other partners. In terms of activity in the caudate nucleus, there was less distinction between positive and negative feedback when interacting with a partner of supposedly high moral character (see also Fouragnan et al. 2013). These results show that, when we decide whether or not to trust someone, information from others is given greater weight than the information we get from direct interactions.

Outside the lab information about the trustworthiness or reputation of others is typically transmitted by gossip. Milinski and colleagues have published a series of
studies demonstrating the powerful effects of gossip on cooperation in groups (e.g. SOMMERFELD et al. 2008). These studies also reveal that people give more weight to gossip than they do to direct observation (SOMMERFELD et al. 2007). This observation accords with the results of the computer tournament described at the beginning of this essay, in which learning by copying others achieved better results than learning directly by trial and error (RENDELL et al. 2010). The reasons are similar. Gossip can be obtained from multiple sources and is therefore based on far more experience than we can achieve on our own. Here again we can benefit from the mistakes of others.

There is, however, a critical difference. When we observe the behaviour of others we are acquiring public information (DANCHIN et al. 2004) that is not actually intended for our consumption. Gossip, in contrast, is a form of deliberate communication. This raises the possibility of cheating if there is an advantage to be gained by spreading gossip that is untrue. Two principles protect us, to some extant, from false gossip. First, as with any form of communication, gossip loses value unless it is mostly true (DAVIDSON 1984). Second, there is protection from the existence of multiple sources of gossip, since false gossip is likely to be in the minority (SOMMERFELD et al. 2008). It is this aspect of human communication that provides, perhaps, the most important evolutionary advance in cognition. Previously it was only possible to change the behaviour of others through various forms of physical manipulation, such as reward or punishment. With the advent of deliberate communication it is possible to change the behaviour of others by changing their beliefs and the way they think. Teaching and deception are at opposite ends of a continuum of the possibilities generated by this ability.

3.4. Changing the way people think.
So far I have considered how instructions from others can tell us about the outside world: which objects are safe, and which should be avoided (FEINMAN et al. 1992), which people to cooperate with and whom to shun (SOMMERFELD et al. 2007). However, instructions can also be used to tell us about the inner world of the mind. We have remarkably poor access to workings of our own minds. Typically, we are only aware of the outcomes of the various subpersonal cognitive mechanisms at
work, with very little awareness of the mechanisms themselves (NISBETT and WILSON 1977). Nevertheless, we are not deterred from talking each other about these mechanisms. For example, we will explain and justify a decision we have just made even though it can be shown these explanations are wrong (HALL et al. 2010; JOHANSSON 1973). Here again we often rely on the reports of others to give us, we hope, a better understanding of our mental life.

My first example comes from studies of ‘ego depletion’. It is widely held that mental effort is like physical effort in the sense that too much exertion will be tiring, making future effort more difficult (BAUMEISTER et al. 1998). But is this really how the mind works? Job and colleagues (JOB et al. 2010) explored the effects of instructions on how people responded to the exertion of mental effort. One group of participants were told ‘working on a strenuous mental task can make you feel tired such that you need a break before accomplishing a new task’. Another group were told ‘sometimes, working on a strenuous mental task can make you feel energized for further challenging activities’. These instructions had striking effects on behaviour. The ‘depleted’ group made more errors on a Stroop task after a period of mental exertion, while the ‘energised’ group made fewer errors.

I suggest that what the instructions were telling participants was how to interpret experiences associated with the exertion of mental effort, perhaps a heightened awareness of action selection or even an increased heart rate. The depletion instructions suggest that these are signs of tiredness and a need for rest. The energizing instructions suggest that these are signs of increased control so that increased effort will not be so costly. In response to such instructions people alter their interpretation of their experiences and act accordingly.

A second example comes from studies of beliefs about free will. Most people believe that nature is not deterministic and that we have control over our actions (NAHMIAS et al. 2005). However, the idea that the experience of free will is an illusion has a long history (SPINOZA 1677). Recently, a number of different groups have started to investigate the effects of beliefs about free will on behaviour. In these studies some participants are presented with statements such as ‘most rational people now
recognise that free will is an illusion' (Crick 1994), while others see statements that
do not involve free will. Participants led to doubt the existence of free will showed
increased aggression and reduced helping behaviour (Baumeister et al. 2009). They
were also more likely to cheat in exams (VoHs and SchooLeR 2008). Effects can be
observed even on more basic aspects of action. It is well established in reaction time
tasks, where participants have to be as accurate and as fast as possible, that
response times increase immediately after an error (see Dutilh et al. 2012 for a
review). This post-error slowing is reduced in participants who have been led to
doubt the existence of free will (Rigoni et al. 2013). Furthermore, the amplitude of
the brain's readiness potential, measured with EEG, which precedes voluntary
responses, is reduced (Rigoni et al. 2011).

These latter observations show how far down the hierarchy of control these top-
down instructions can penetrate. They also suggest an explanation for the effects on
high levels of behaviour such as cheating. It appears that people equate free will with
a mechanism for the top-down, intentional control of behaviour (Rigoni et al. 2013).
Post-error slowing depends upon metacognitive processes required to monitor
behaviour for errors, and then exert control on the processes generating behaviour
by increasing caution. If we don't have such top-down control (i.e. free will), then
there is no value in exerting effort to monitor our behaviour. A similar argument
would lead to the increase in cheating and the reduction in helpfulness. Our basic
urge is to be selfish; to gain advantages at the expense of others. To overcome this
urge we have to exert self control. It is this intentional, top-down control that
enables us to behave in a moral fashion. If we don't have such top-down control then
we might as well give in to our basic urges and gain all the (short term) advantages
that this might bring.

3.5 Free will and responsibility: the role of culture

But where does this idea that our basic urge is to be selfish come from? Is it actually
correct? There is some evidence that the prosocial behaviour that most of us show
towards our fellows is automatic and does not depend upon top-down control
(Haruno and Frith 2010; Rand et al. 2012). In one experiment it was found that
interfering with top-down control did not increase selfish behaviour, but reduced it
I suggest that these results show that we have consensus position about the mental control of action, which may not always be correct.

Given the belief that free will depends upon top-down control, that is the executive processes associated with working memory - sometimes referred to as system 2 (Evans 2003) - we would expect the exertion of free will to be closely linked with consciousness. This is indeed the case. When behaviour is caused by conscious states, people tend to judge that the agent acted freely. In contrast, when behaviour is caused by unconscious states, people judge that the agent did not act freely (Shepherd 2012). Our beliefs about free will are also intimately connected with the idea of responsibility (Nahmias et al. 2005) We can be held responsible for our actions if these have been chosen freely. Responsibility has a major role in western legal systems. If we are capable of controlling our impulses, then we are responsible for our actions. If, by reason of mental illness, for example, we are not capable of controlling our actions, then our responsibility is diminished. Children and animals are also considered unable to exert control and are therefore not considered responsible for their actions. However, this is a relatively recent development. In medieval times animals such as pigs and even insects were tried in court (Humphrey 2002), and even today the age at which children become legally responsible for their actions varies widely even within Europe (Hazel 2008).

These variations are consistent with the idea that culture plays a large role in our beliefs about free will and the control of action. If this is indeed the case, then we might expect to find other cultures where people have different ideas about responsibility and the control of action. This seems to be the case among the Mopan Mayas of Central America (Danziger 2006). In this culture perpetrators of crimes are punished according to the degree of damage that they have caused, rather than the degree to which the act was committed intentionally.

I have suggested that the consensus in western cultures, that to behave well, we must exert top-down conscious control of our selfish urges, may not be an accurate account of how the mind works. Nevertheless this consensus plays an important
role in maintaining social cohesion. Experimental studies of economic exchanges show how easily cooperation within groups can be subverted by the appearance of free riders, people who benefit from the willingness of others to share resources, while not sharing themselves. Cooperation can be maintained by the introduction of sanctions through which free riding is punished (Fehr and Gächter 2002). Furthermore people prefer to join institutions in which such sanctions are applied (Gürerk et al. 2006). However, punishment is only applied when it is believed that the free riders are acting deliberately of their own free will. Punishment (or reward for good behaviour) was not applied to people believed to be behaving in accord with instructions given by the experimenter, even though the consequences of their behaviour was no different (Singer et al. 2006).

The idea that the experience of free will, namely, it is I that am causing the action, is the basis for moral responsibility goes back at least as far as Epicurus (Bobzien 2006). Epicurus also believed that we acquire the idea that we are responsible causal agents through the observation that human beings, including ourselves, are praised and blamed for their actions. Such instructions create knowledge of how to place responsibility. However, the research I have outlined above suggests that these instructions can also change the way we experience our actions. I have already noted that people, led to doubt the existence of free will, show a reduced amplitude of brain’s readiness potential (Rigoni et al. 2011). Instructions can also alter the experience of ‘intentional binding’. Intentional binding is an experience of the timing of actions. It provides a marker to distinguish voluntary from involuntary acts. With a voluntary action the time between the action and its outcome is experienced as being shorter (Haggard et al. 2002). However, when participants are told that they were causing an action that was actually involuntary, they have a stronger experience of intentional binding (Dogge et al. 2012). This suggests that it is not only our ideas about free will that are culturally determined, but also our experience of free will.

3.6 Two minds are better than one

I have shown how teaching and gossip can provide ‘stories’ about how the mind works and that these stories alter our behaviour and our experience. These effects
have all been at the level of the individual. However, we have the ability to tell each other about how our minds work, and this enables a special kind of joint action that is uniquely human. It has long been known that decisions based on the knowledge of many can be better than the decisions of any single individual. This is the basis of Condorcet’s jury theorem (CONDORCET 1785/1994): As long as everyone has a better than chance probability of making the correct decision, however small that probability may be, then the joint decision of group will have a higher probability of being correct. A similar effect was demonstrated empirically by Galton (GALTON 1907). He recorded the answers given by people attending a country fair and trying to guess the weight of a bull. He showed that the average of these guesses was very close to the true weight of the bull and closer than the best individual guess. There is, however, no interaction involved in these examples. The information from many individuals is simply pooled by an external agent.

We have recently been studying joint decision making in situation where the people come to a joint decision through discussion (BAHRAMI et al. 2010). In one of these experiments participants worked in pairs trying to detect a weak visual signal that could occur in one of two time intervals. After making independent decisions they compared their choices and, if they disagreed, reached a joint decision through discussion. As long as the pairs had reasonably similar perceptual abilities, these joint decisions were significantly more accurate than the decisions of the better performing individual in each pair. In additional experiments we showed that this group advantage disappeared if the pairs did not discuss their decision, but simply took it in turns to make the final decision. On the other hand, the group advantage still emerged, although more slowly, when the pairs were given no feedback as to whether the final decision was right or wrong (BAHRAMI et al. 2012). These results confirm that people can enhance their abilities by sharing their perceptions and suggest that discussion, independent of feedback about performance, may have a critical role in such enhancement (see also BAHRAMI et al. 2013). It may this enhancement that provides the evolutionary pressure to increase the ability to share experiences (SHEA et al. in press).
To explore the mechanisms by which this sharing is achieved we took advantage of recent developments in the mathematical modelling of decision making. In particular we considered the mechanism by which information from two senses is combined within a single brain. An example would be combining vision and touch in order to estimate the height of an object (Ernst and Banks 2002). Such studies suggest that the nervous system optimises the decision by taking into account the reliability (or precision) of each sense and giving greater weight to the sensory signal with the greater reliability (Ernst and Bülthoff 2004). We explored whether, by analogy with this mechanism, when information is combined from two people, greater weight would be given to the person with greater reliability, on a trial by trial basis. Such reliability could be communicated in terms of the confidence each participant had on what they had just seen. By estimating individual reliability from their individual performance we confirmed that our pairs were indeed functioning close to the optimum (Bahrami et al. 2010).

We then explored how this reliability was communicated by looking in detail at what was said during the discussions (Fusaroli et al. 2012). We confirmed that participants were indeed talking about confidence and were developing novel verbal scales for communicating their degree of confidence on each trial. Furthermore the group advantage achieved by each pair was greater if they restricted their talk to discussion of confidence, and particularly, if they had developed a stable set of verbal expressions to share and compare levels of confidence.

These studies show that we can not only share the experience of motor control, but that we can also share and discuss our sensory experiences. They also suggest how the uniquely human ability to share with others what goes on in our minds enables us to solve problems that are beyond the abilities of individual thinkers. I believe that it is this ability to share experiences that is fundamental to the emergence of cumulative culture. By discussing and learning from others how to think we can not only create ways of controlling our actions and thus enhance cooperation within groups, we can also learn from the experiences of others how to make increasingly accurate accounts of the world and of ourselves. Indeed it is the codification of this latter process that is the basis of the scientific method.
4.0 Culture and the brain

We know very little as yet about the brain mechanisms that enable us to reflect upon our experiences and discuss them with others. However, in the last few years there has been increasing interest in exploring the neural correlates of one component of such reflection: metacognition. Metacognition, sometimes defined as thinking about thinking, has been studied experimentally in relation to memory, action and perception (Metcalfe and Shimamura 1994). In relation to memory, for example, participants might be asked to predict how well they will remember the words from the list they have just learned. In the case of action they might be asked to what extent they were in control. In the case of perception they might be asked how confident they were in their report of what they had just seen. All these cases involve reflecting upon one's mind and then reporting the results of such reflection. In the case of perception, techniques derived from signal detection theory have been developed for precise measurement of metacognitive ability (Maniscalco and Lau 2011). Rather than measuring the accuracy with which a participant can detect a sensory signal (d-prime), we measure the accuracy with which the participant can estimate whether he has given the correct answer (meta d-prime). These two measures can dissociate. Individuals can be good at detecting signals, while not being good at knowing whether they are right or wrong.

Fleming and colleagues (Fleming et al. 2010) looked for correlations between brain structure and perceptual metacognitive ability in a group of participants who were matched for perceptual ability. They found that metacognitive ability was correlated with gray matter volume in the anterior prefrontal cortex (Brodmann area 10). The same brain region has also been linked with metacognition in functional brain imaging studies: confidence in perceptual decision making (Fleming et al. 2012), confidence in recognition memory (Yokoyama et al. 2010) and judgment of control of action (Miele et al. 2011). The same brain region has also been implicated in the mechanism by which instructions, i.e. top-down control exerted by others, have effects on beliefs and behaviour (Fouragnan et al. 2013).
The medial wall of the right hemisphere of the human brain is shown embedded in Talairach coordinate space. The stippled area is the approximate location of Brodmann area 10 in fronto-polar cortex. The numbered circles are the locations of activity associated with tasks involved metacognitive processes. 1) Awareness of perceptual accuracy (FLEMIN et al. 2010). 2) Awareness of agency (MIELE et al. 2011). 3) Applying prior knowledge of trustworthiness (FOURAGNAN et al. 2013). 4) Confidence in recognition memory (YOKOYAMA et al. 2010).

There is some evidence that Brodmann area 10 showed marked evolutionary development in humans. Area 10 in the human brain is larger relative to the rest of the brain than it is in the apes, and its supragranular layers have more space available for connections with other higher-order association areas. This suggests that the neural substrates supporting cognitive functions associated with this part of the cortex became enlarged and specialized during hominid evolution (SEMENDEFERI et al. 2001).

These are very preliminary results. Discovering that this particular brain area is important for enabling cultural effects is only a first step in elucidating the mechanism by which this happens. It is also important to note that this is not a one-way process. The emergence of human culture depended upon the evolution of brain
mechanisms that supported novel cognitive processes. But at the same time the emergence and development of human culture alters the human brain.

It is likely that, over the last ~40,000 years, there has been little change in the brain with which all humans are endowed (Forster 2004; Mellars 2006). But, now that we know just how plastic the brain can be, it is likely that dramatic changes occur in each brain during the course of development. That even the structure of the adult human brain can be altered by practice and experience is demonstrated by studies of taxi drivers learning how to navigate through the streets of London. A 4-year longitudinal study of people training to become licensed London taxi drivers revealed that success in this endeavour was associated with a selective increase in gray matter volume in the posterior hippocampus (Woollett and Maguire 2011). These effects on brain structure can occur quite rapidly. For example, seven days practice of a three ball juggling task was sufficient to generate detectable changes in grey matter density in the extra-striate visual cortex (Driemeyer et al. 2008).

These examples involved rather specialised skills, but it is a feature of human culture that we all acquire a great many skills in the course of our lives, some specialised and some universal. Literacy is an example of skill created by human culture, which has appeared far too recently to have had any effect on the evolution of the brain. Indeed, literacy did not begin to approach a universal human skill until about two hundred years ago. Nevertheless, as we would expect, the acquisition of literacy generates detectable changes in brain structure and function (Carreiras et al. 2009). There are undoubtedly many other skills that we acquire through upbringing and culture. Many of these will be concerned with social interactions (Herrmann et al. 2007), such as the skill of attributing responsibility that I discussed in section 3.5. It is also likely that practice could increase the accuracy of introspection, leading to an increase in grey matter density in BA10 (Fleming et al. 2010). Since acquisition of all of these many skills will have an effect on brain structure and function, it is likely that the brain of a contemporary adult human will look distinctly different from that of an ancestor of thousands of years earlier. These differences in the brain are created by culture.
In part 3 of this essay I outlined the cognitive abilities instantiated in the brain and possibly unique to humans, which enable the emergence of cumulative culture. In a sense it is these brain processes that create culture. I suggested that our interactions with the world, both physical and mental, depend upon a process of hypothesis testing in which prior expectations and beliefs are continuously modified through the evidence from our senses. This is essentially a loop in which top-down processes (prior beliefs) and bottom-up processes (sensory evidence) are equally important. There is, however, a hierarchy of such loops with those at the top being concerned with more abstract and long-term properties of the world. Cumulative culture is possible because the highest loop in this hierarchy extends beyond the individual mind. In this loop the prior expectations come from other minds thereby creating shared narratives about how the mental and physical worlds work. As a result of this loop, even though it is brain processes that enable culture to emerge, at the same time the emergence of cumulative culture alters the functioning of the human brain.

Bibliography


1 A strikingly similar two-route system has been observed for print reading in English. The problem here is to translate a string of letters seen by the visual system into a sound generated by the motor system. The indirect route is needed for reading irregular words (e.g. yacht) where the pronunciation has to be learned for each word. In this case the letter string is converted to a meaning, which is then converted to a sound. The direct route is needed for reading pronounceable non-words (e.g. yash), where there is no learned meaning available to guide pronunciation. In this case grapheme-phoneme conversion rules must be used to convert the letter string directly into sounds COLTHEART, M., K. RASTLE, C. PERRY, R. LANGDON, and J. ZIEGLER: DRC: a dual route cascaded model of visual word recognition and reading aloud. Psychol Rev 108, 204-256 (2001), TAYLOR, J. S., K. RASTLE, and M. H. DAVIS: Can cognitive models explain brain activation during word and pseudoword reading? A meta-analysis of 36 neuroimaging studies. Psychol Bull 139, 766-791 (2013).

2 Not all our basic urges are selfish, but it is all too easy to come up with justifications for exerting top-down control to overcome automatic prosocial behaviour (e.g. you should not help the poor because this will make them more feckless).