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Abstract:

Our decisions are affected not only by objective information about the available options but also by other people. Recent brain imaging studies have adopted the cognitive neuroscience approach for studying the neural mechanisms of social influence. A number of studies have shown that social influence is associated with neural activity in the medial prefrontal cortex and ventral striatum, which are two brain areas involved in the fundamental and not exclusively social mechanisms of performance monitoring. Therefore, the neural mechanisms of social influence could be deeply integrated into our general neuronal performance-monitoring mechanisms.

Keywords: Conformity; fMRI; Medial prefrontal cortex; Neuroimaging; Persuasion; Reinforcement learning; Social influence; Ventral striatum

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Biographical Sketch



Vasily Klucharev received his PhD in physiology from Saint Petersburg State University in 2000. Klucharev is an expert in neuroeconomics mechanisms of social influence on human decision-making. He has published widely in neuroscience journals such as *Neuron*, *Journal of Neuroscience*, and *SCAN*. Klucharev had been involved as a researcher at the Laboratory of Computational Engineering, Helsinki University of Technology (2000–2004); Erasmus Research Institute of Management (Rotterdam); and Donders Institute for Brain, Cognition and Behaviour (2004–2009). He has been a senior researcher and lecturer at the University of Basel since 2009 and a professor and [dean of the Faculty of Psychology](#) at the Higher School of Economics, Moscow.



Anna Shestakova, PhD, studies cognitive neuroscience, neurobiology of decision making and language. Anna earned her PhD in psychology at the University of Helsinki (Finland) and continued to gain expertise in world-leading research centres: BioMag Laboratory at the Helsinki University Central Hospital, Functional Imaging Laboratory at UCL, Centre for Speech and Language at the University of Cambridge and MEG Laboratory of the MRC Cognition and Brain Sciences Unit in Cambridge. Since 2013 Anna Shestakova acts a Director of the Centre for Cognition & Decision Making at the National Research University Higher School of Economics, Moscow.

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Social Influence and Persuasion and Message Propagation

V Klucharev and A Shestakova, Higher School of Economics, Moscow, Russia

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Abbreviations

dt0010
dt0015

fMRI Functional magnetic resonance imaging
FRN Feedback-related negativity

pMFC Posterior medial prefrontal cortex
TMS Transcranial magnetic stimulation

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Neuroscience of Social Influence

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For a long time, cognitive neuroscience has primarily investigated single individuals to uncover the neuronal mechanisms of individual decision-making. However, our decisions are often affected by the decisions of others (Ajzen & Fishbein, 1980; Cialdini & Goldstein, 2004). For example, humans demonstrate various forms of herding – alignments of the thoughts or behaviors of various individuals into a group (herd) without centralized coordination (Raafat, Chater, & Frith, 2009). Only relatively recently has the profound role of social influence been acknowledged by the newer fields of neuroscience, namely, social neuroscience and neuroeconomics (for a review, see Izuma, 2013). However, the idea that the ‘individual decision’ is normally generated by a network of individuals (multiple brains) rather than by a single individual remains marginally popular. Here, we suggest that the values underlying our choices are dynamic products of the brain activity of multiple individuals. Furthermore, we argue that individuals routinely adjust their opinions and decision values so that they are in line with the group opinion based on a fundamental (and not exclusively social) learning mechanism. This idea is similar to the concept developed recently in psychology (e.g., Heyes, 2012).

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Social psychology has convincingly demonstrated that the social environment has profound effects on human behavior (Ajzen & Fishbein, 1980; Cialdini & Goldstein, 2004). Some psychologists even go further to claim that human beings display ‘superorganismic’ properties (Keseb, 2012). The effect of others’ opinions on individual behavior is known as *social influence*. Every day, we are surrounded by attempts to influence us that are both explicit and implicit. The effects of group opinion on individual judgments and decisions have been robustly replicated since Solomon Asch’s pioneering work on the line-judgment conformity experiments, in which many participants conformed to the erroneous majority opinion that two lines were of the same length when in reality they were different in length by several inches (Asch, 1951). Here, we suggest that the mechanisms of social influence are deeply integrated into the fundamental neural performance-monitoring mechanisms. More specifically, we suggest that social influence engages neural mechanisms that are similar to reinforcement learning. In particular, we argue that deviations from group behaviors are treated by the nervous system as negative outcomes or reward prediction errors. We also provide an overview of recent neuroimaging studies that have investigated the neurobiological mechanism of social influence with a focus on conformity.

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Neurobiological Mechanisms of Conformity

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Conformity is a particular form of social influence in which individuals align their attitudes, beliefs, and behaviors with other members of a reference group in the absence of an explicit order or request. It has been suggested that conformity is driven by two types of social norms: (1) *injunctive norms*, which have a moral tone and characterize what people should do, and (2) *descriptive norms*, which represent typical behavior or what most people actually do in a particular situation regardless of its appropriateness (Cialdini & Goldstein, 2004). It is not surprising that people have a tendency to conform to injunctive norms (e.g., ‘Do not drink and drive’) since they are often reinforced by different forms of punishment. In contrast, descriptive norms represent information about peoples’ dominant behavior and thus have a more informational nature.

Nevertheless, descriptive norms (or social validation) are surprisingly effective. They have a strong influence on whether people pay their taxes, teenagers commit a crime, spouses commit infidelity, or households adopt environmentalist policies (Cialdini & Goldstein, 2004; O’Keefe, 2002). Interestingly, we are usually not aware of the strong influence of descriptive norms; rather, we have a strong hidden tendency to follow others (Bryan & Test, 1967). Whereas psychological studies emphasize the rewarding value of social approval or affiliation with others (Cialdini & Goldstein, 2004), behavioral economics studies focus more on the effects of being punished for violating the norm (Fehr & Fischbacher, 2004a). In fact, both approaches may suggest that conformity to social norms is underlined by a reinforcement learning mechanism, that is, social norms selectively reinforce certain behaviors. Thus, social comparison leading to conformity could be integrated into the performance-monitoring mechanism, in which successful behavioral patterns are reinforced, while errors call for adjustments of behavior (Montague et al., 2006).

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Recent brain imaging studies have utilized the cognitive neuroscience approach for analyzing the neural mechanisms of social conformity. A pioneering study investigated the effect of group pressure during a mental rotation task and found that conformity/independence was associated with the striatum activity, among other brain regions (Berns et al., 2005). Anatomical, electrophysiological, and brain imaging studies have clearly shown that the ventral striatum participates in – and perhaps mediates – goal-directed behaviors by encoding expected values and playing a critical role in reward processing and reinforcement learning (Carelli, 2002; Knutson & Wimmer, 2007).

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p0060 The authors of another study hypothesized that a perceived deviation from group norms triggers a neural response that is fundamentally similar to the reward prediction error in reinforcement learning, thereby indicating a need to change individuals' future behavior in line with group norms (Klucharev et al., 2009). Many reinforcement learning models include a 'reward prediction error,' which is the difference between the expected outcome and the actual obtained outcome (Rescorla & Wagner, 1972). The reward prediction error guides decision-making by signaling the need for an individual to adjust her behavior. The reinforcement learning theory of performance monitoring suggests that activity in the posterior medial prefrontal cortex (pmFC), which is a rostral part of the cingulate cortex, indicates whether the outcome of an action is better or worse than expected (Holroyd & Coles, 2002). Thus, activity in the pmFC signals the reward prediction error.

p0065 However, the pmFC is not alone in monitoring behavioral outcomes. In fact, a growing body of research has identified a distributed neural network, including the ventral striatum, that is involved in this process. If conformity is indeed based on an 'automatic' mechanism of reinforcement learning, a conflict with group opinion should trigger a prediction error-like response that is manifested in activity of the pmFC and the ventral striatum. The strength of this activity should then predict social conformity.

p0070 To test this hypothesis, Klucharev et al. (2009) designed a conformity task in which the subject's initial judgments of

facial attractiveness were open to influence by group opinion. During functional magnetic resonance imaging (fMRI) brain scanning (first session), the female subjects rated the attractiveness of various female faces. After each rating, they were informed of the average opinion of the other female subjects (i.e., the 'group rating'). The actual group ratings were systematically manipulated during the experiment: Sometimes, the group was more positive about the face than the subject; sometimes, it was more negative; and sometimes, the group agreed with the subject. Thus, this procedure introduced systematic conflicts between the subject's own judgment and the normative group opinion. To identify subsequent conformity with the group, subjects rated the same set of faces again 30 min after the fMRI brain scanning session (second session). Behavioral results showed that subjects adjusted their attractiveness ratings to align them with the group ratings, thereby conforming to the group. A conflict with group opinion activated the pmFC and deactivated the ventral striatum. These results suggest that conformity is an automatic process in which people form their own opinion, become aware of the group opinion, and then quickly shift their opinion to make it more compliant with the group. In the conformity task, the subjects did not have any rational reason to change their own judgments (e.g., the group was not physically present so they could not punish or ridicule the subjects' opinion); nevertheless, the subjects repeatedly conformed to the group opinion (Figure 1).

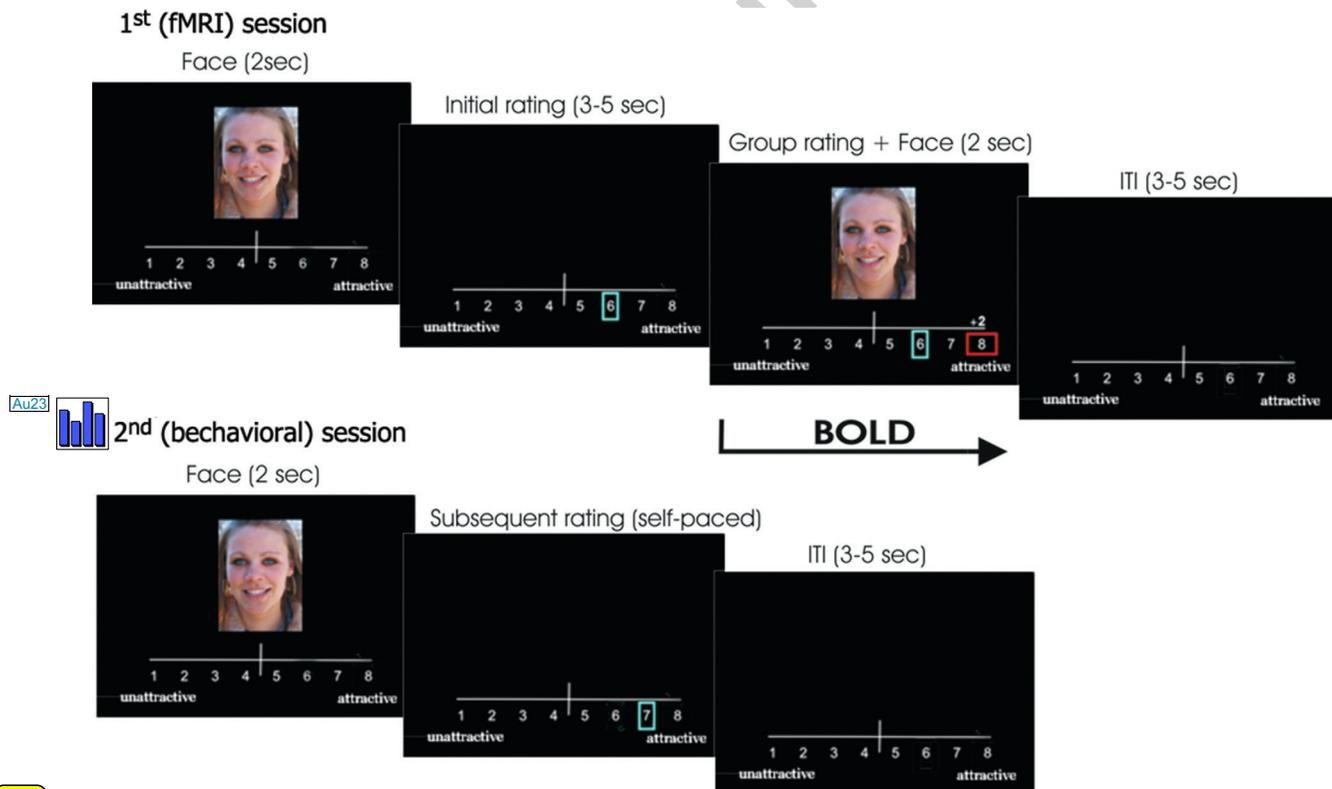
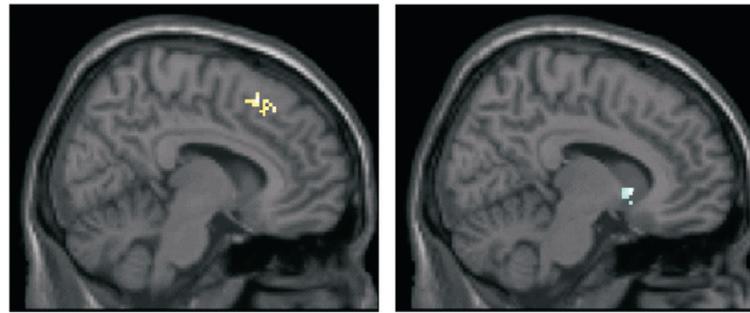


Figure 1 The conformity task. During first session, the subjects rated the attractiveness of various faces. After each rating, they were informed of the average opinion of the other female subjects (i.e., the 'group rating'). Thus, conflicts between the subject's own judgment and the normative group opinion were systematically evoked. Subjects rated the same set of faces again 30 min later during second session in order to detect conformity. Adapted from Klucharev et al. (2009), with permission.



0015 **Figure 2** Both the conflict with group ratings and the subsequent conformity activated the pmFC (left part of the figure) and deactivated the ventral striatum (right part of the figure) (the results of the conjunction analysis). Adapted from Klucharev et al. (2009), with permission.

0075 To further study the role of the pmFC in social influence, repetitive transcranial magnetic stimulation (TMS) was used to modulate social conformity to group opinion (Klucharev, Munneke, Smidts, & Fernandez, 2011). The results demonstrated that the transient downregulation of the posterior medial frontal cortex by TMS reduced conformity, as indicated by reduced conformal adjustments in line with group opinion. Both the extent and the probability of the conformal behavioral adjustments decreased significantly in relation to a sham and control stimulation over another area of the brain. Taken together, the results imply that pmFC downregulation reduces conformity by attenuating the effect that a conflict with a normative group opinion has on behavior (Figure 2).

0080 A number of fMRI experiments have shown that social influence is associated with neuronal response in the pmFC and ventral striatum, two brain areas involved in the monitoring of behavioral outcomes (Behrens, Hunt, Woolrich, & Rushworth, 2008; Berns, Capra, Moore, & Noussair, 2010; Campbell-Meiklejohn, Bach, Roepstorff, Dolan, & Frith, 2010; Falk, Berkman, Mann, Harrison, & Lieberman, 2010; Klucharev et al., 2009). Interestingly, the pmFC has prominent connections with the ventral striatum (Groenewegen, Room, Witter, & Lohman, 1982; Hauber & Sommer, 2009; Parkinson, Willoughby, Robbins, & Everitt, 2000). Furthermore, disconnecting the pmFC from the ventral striatum has been found to impair decision-making and stimulus-reward learning in animals (Hauber & Sommer, 2009; Parkinson et al., 2000). A downregulation of the pmFC could perturb the entire network underlying performance monitoring and social learning; could influence reinforcement learning mechanisms; and, as a consequence, could affect conforming behavioral adjustments.

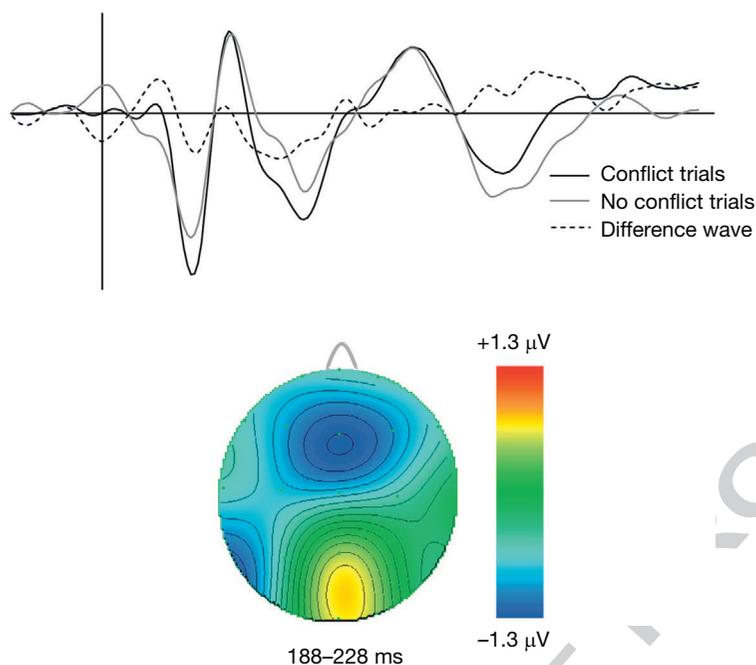
0085 A 'reward prediction error' signal at the pmFC can be measured as a negative event-related potential (ERP) on the scalp that has been called feedback-related negativity (FRN; see Cohen & Ranganath, 2007; Miltner, Braun, & Coles, 1997). Several ERP studies have demonstrated that a mismatch between individual opinion and the opinion of the group triggers FRN (Chen, Wu, Tong, Guo, & Zhou, 2012; Kim, Liss, Rao, Singer, & Compton, 2012; Shestakova et al., 2012). The FRN amplitude tends to correlate strongly with a negative prediction error and only marginally with a positive prediction error (Chase, Swainson, Durham, Benham, & Cools, 2011). Importantly, FRN is often associated with performance monitoring and the subsequent adjustment of behavior (e.g., Cohen & Ranganath, 2007). In general, FRN is a negative shift in the

ERP that occurs within 200–400 ms after an individual receives negative performance feedback (Miltner et al., 1997). Both source localization and fMRI studies have confirmed that FRN is generated in the pmFC (Gehring & Willoughby, 2002; Nieuwenhuis, Holroyd, Mol, & Coles, 2004; Nieuwenhuis, Schweizer, Mars, Botvinick, & Hajcak, 2007; Nieuwenhuis et al., 2005). Shestakova et al. (2013) tested the hypothesis that conflicts with a normative group opinion evoke an FRN. Indeed, they found that a conflict with a normative group opinion triggered a cascade of neuronal responses: from an earlier FRN response reflecting a conflict with the normative opinion to a later ERP component that peaked at 380 ms and reflected a conforming behavioral adjustment (Figure 3).

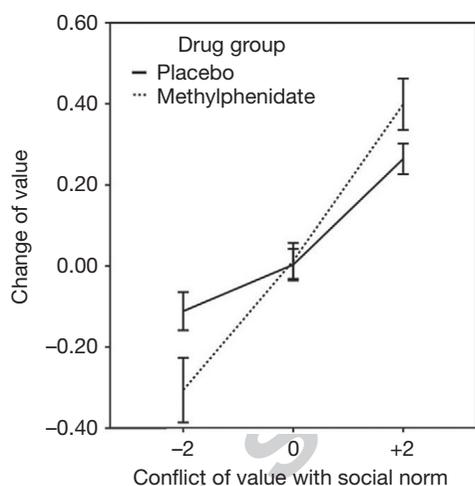
In line with the proposed role of the pmFC in performance monitoring, the magnitude of the pmFC activity has been shown to predict the strength of subsequent behavioral adjustments during simple decision-making (Cohen & Ranganath, 2007; Kerns et al., 2004; O'Doherty, Critchley, Deichmann, & Dolan, 2003). The ventral striatum and prefrontal cortex receive extensive dopaminergic projections (Fields, Hjelmstad, Margolis, & Nicola, 2007). The reinforcement learning theory of performance monitoring suggests that the pmFC activity is modulated by a dopamine-related neural signal, which indicates whether the outcome of an action is worse or better than expected (reward prediction error) regardless of the primary cause of the deviation from the prediction (Holroyd & Coles, 2002; Matsumoto, Matsumoto, Abe, & Tanaka, 2007). Thus, according to the reinforcement learning hypothesis of social influence, the amount of dopamine in the pmFC should modulate conformity.

Campbell-Meiklejohn et al. (2010) used methylphenidate, a dopamine and noradrenaline agonist, to modulate conformity. Healthy adult females received either a single oral dose of methylphenidate or a placebo. The methylphenidate group exhibited twice the conformity effect of the placebo group following moderate social conflict during the conformity task, but not after large conflicts. These results suggest that methylphenidate might enhance signals that would otherwise be too weak to evoke conformity. Overall, the results of this study give additional support for the reinforcement learning hypothesis, which suggests an involvement of the dopamine-related performance-monitoring system in the mechanisms of social influence (Figure 4).

So far, many studies have indicated an involvement of the pmFC and ventral striatum in neural mechanisms of social



0020 **Figure 3** The conflicts between the subject's own judgment and the normative group opinion evoked FRN, which is often associated with a general mechanism of performance monitoring and the subsequent adjustment of behavior. Adapted from Shestakova et al. (2013), with permission.



0025 **Figure 4** Subjects treated with methylphenidate, a dopamine and noradrenaline agonist, conformed more following moderate social conflict. Adapted from Campbell-Meiklejohn, D. K., Simonsen, A., Jensen, M., Wohlert, V., Gjerløff, T., Scheel-Kruger, J., et al. (2012). Modulation of social influence by methylphenidate. *Neuropsychopharmacology*, 37(6), 1517–1525, with permission.

influence (e.g., Behrens et al., 2008; Berns et al., 2010; Campbell-Meiklejohn et al., 2010; Falk et al., 2010; Klucharev et al., 2009). For example, the influence of a peer group on adolescents' music preferences was associated with activity in both regions (Berns et al., 2010). In this study, the ventral striatal activity decreased when the subjects changed their rating to conform to the group opinion. Furthermore, the more participants were influenced by their peers' opinions, the more the activity in the pmFC and insular cortex was modulated by

others' opinions. The authors of this study therefore suggested that conformity could be evoked by generating 'social mismatch' anxiety and a cognitive/emotional dissonance.

As we already mentioned, social psychology studies have shown that our preferences are indeed strongly influenced by others but that this effect depends on how we feel about those people. Izuma and Adolphs (2013) manipulated preferences for material goods by telling participants the preferences of strongly liked or disliked social groups. After the subjects rated T-shirts according to their preference, they were exposed to the ratings of others students (the liked group) or sex offenders (the disliked group) for the same T-shirts. The participants' preferences conformed to those of the liked group and diverged from the disliked group. Similar to previous studies, the authors found that activation of the pmFC tracked the discrepancy between individual preferences and group preferences. Furthermore, activity of the pmFC was associated with conforming preference changes (toward the liked group and away from the disliked group), which were tested up to several months after exposure to the social influence. Izuma (2013) suggested that a mechanism that recruits the pmFC may reflect the aversive nature of the neural mechanism underlying conformity and this mechanism is similar to cognitive dissonance. The results could indicate that the pmFC tracks the degree of cognitive imbalance (Heider, 1958) on a trial-by-trial basis, where 'imbalance' is created by a cognitive inconsistency among self, other people, and an object (e.g., 'I like it, but my friends do not like it'). Izuma (2013) concluded that pmFC activation could be a marker of cognitive inconsistency or, in other words, a neural 'dissonance thermometer' (Figure 5).

Overall, three main neural mechanisms have been proposed for social influence: (1) the *social mismatch anxiety* mechanism that triggers emotional dissonance encoded in the

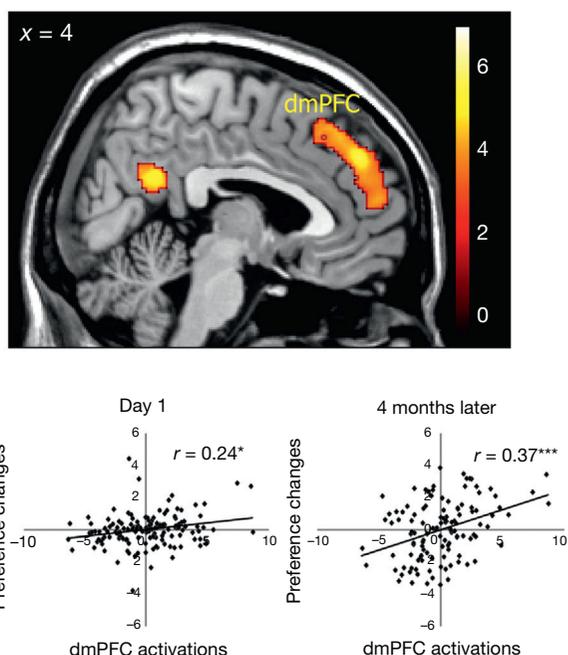


Figure 5 Activity in the pMFC regions significantly correlated with the degree of conflicts between the subject's own judgment and the normative group opinion (upper part of the figure). Furthermore, activity of the pMFC significantly predicted subsequent conformity: several minutes after viewing others' preferences (day 1) and even after 4 months. Adapted from Izuma, K., & Adolphs, R. (2013). Social manipulation of preference in the human brain. *Neuron*, 78(3), 563–573, with permission.

insular cortex (Berns et al., 2010), (2) *cognitive inconsistency* encoded in the pMFC (Izuma, 2013), and (3) the *reinforcement learning mechanism* (Klucharev et al., 2009; Montague & Lohrenz, 2007), which suggests that individuals adjust their intrinsic decision values so that they are in line with the group opinion based on a fundamental (and not exclusively social) learning mechanism implemented in the pMFC and ventral striatum.

Neurobiology of the Internalization of Social Influence

Zaki, Schirmer, and Mitchell (2011) used the conformity task to investigate whether social influence changes intrinsic preferences. The participants of this study were first exposed to the group ratings while rating facial attractiveness (during first session of the conformity task) but were scanned while they rated the faces a second time (with no group ratings, i.e., during second session of the conformity task). Similar to previous studies, the behavioral results demonstrated that the participants changed their ratings to conform to the group opinion. The social influence was accompanied by modulated activity in two brain regions associated with coding subjective value – the ventral striatum and the orbitofrontal cortex. Thus, exposure to social norms modulated the participants' neural representations of value assigned to stimuli.

Campbell-Meiklejohn et al. (2010) investigated the influence of reviewer opinions of music on adults. When a person was influenced by the experts' opinion, the magnitude of the

ventral striatum response to that object's value changed accordingly. These findings indicate that social influence on the value of an object is associated with the magnitude of the ventral striatum response to receiving it. It suggests that social norms change intrinsic preferences and modulate very basic value signals in the reinforcement learning circuitry.

Here, we argue that the mechanism of the social influence is integrated into the fundamental neural performance-monitoring mechanisms: deviations from group behaviors are treated by the nervous system as negative outcomes, generating reward prediction errors. Behrens et al. (2008) demonstrated that social information may be acquired using the same associative processes assumed to underlie reward-based learning. In their study, the subjects performed a decision-making task that required the combination of individual learning with another player's advice. Two neighboring subregions of the pMFC were central to learning about social- and reward-based information and for determining the extent to which each source of information guides behavior. Their findings further support the hypothesis that human conformity can be underlined by the same associative processes previously established for learning nonsocial features; that is, the dopamine-related activity of the pMFC and the ventral striatum encodes the reward prediction error signal evoked by perceived deviations from others.

Neurobiology of Other Forms of Social Influence

A limited number of studies have investigated the neural mechanism of other forms of social influence (Edelson, Sharot, Dolan, & Dudai, 2011; Falk, Berkman, & Lieberman, 2012; Falk, Morelli, Welborn, Dambacher, & Lieberman, 2013; Falk, O'Donnell, & Lieberman, 2012; Klucharev, Smidts, & Fernandez, 2008; Stallen, Smidts, Rijpkema, Smit, & Klucharev, 2010). One neuroimaging study examined neural activity evoked by more effective (high-tailored) smoking-cessation messages in comparison to less effective (low-tailored) smoking-cessation messages (Chua, Liberzon, Welsh, & Strecher, 2009). The activity of the pMFC and ventral MFC was enhanced by the more effective antismoking arguments. Another study demonstrated that neural responses in the ventral MFC to persuasive messages promoting a telephone hotline for helping people quit smoking predicted variability in behavioral changes in the subsequent week (Falk et al., 2011). A new interesting line of research has focused on the brains of persuaders (Falk et al., 2013): exposure to information that was subsequently promoted by persuaders more enthusiastically has been found to be associated with increased neural activity in the pMFC, the ventral striatum, the ventral MFC, and other brain regions of persuaders (Falk, Berkman, et al., 2012; Falk, O'Donnell, et al., 2012). Therefore, activity in the ventral striatum and ventral MFC of effective of persuaders could indicate a rewarding nature of sharing the persuasive information with others.

In neuroimaging studies that have investigated conformity, others' opinion was normally presented after participants expressed own private opinion. A number of studies have investigated the impact of social advice presented before a participant makes a decision. These studies have highlighted an important role of the ventral MFC in social influence, the region that has been previously associated with 'decision

value,' which is a subjective expected value of the chosen option at the time of choice (Chib, Rangel, Shimojo, & O'Doherty, 2009). The ventral MFC was also associated with fast emotional learning (Roitman & Grabenhorst, 2008). For example, in one fMRI study, participants received advice from a randomly selected advisor in a version of the Iowa Gambling Task, which is widely used for studying emotion-based learning (Biele, Rieskamp, Krugel, & Heekeren, 2011). The participants repeatedly chose from four card decks and received feedback after each trial. Advice regarding which option the participant should choose was received before participant made an individual decision. Advices had a significant influence on their learning processes, and a neural 'outcome-bonus' signal (greater activity following the advice) was noted in the ventral striatum and ventral MFC that indicated a greater reaction to the positive and negative feedbacks after the recommended choices compared to the nonrecommended choices.

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In another study by Burke, Tobler, Baddeley, and Schultz (2010), participants were engaged in an observational learning task based on a simple two-armed bandit problem. However, before the participants made their choices, they were able to observe the behavior of another player. Thus, the participants could observe the other player's actions and outcomes and also learn from their own actions. When the participants observed the actions and the outcomes of another player, they chose the correct stimulus more often than when only another player's actions were observable. The ventral MFC and ventral striatum coded the observational outcome prediction errors during the outcome of the other player. Thus, various studies have found that social influence can be underlined by the fundamental learning processes previously established for learning other nonsocial features of the environment.

p0145

In sum, our decisions are affected not only by objective information about the choice options themselves but also by the perceived behavior of others. This strategy is often effective, and it is probably based on an evolutionary mechanism. An 'evolutionarily stable strategy' is a strategy that, if most members of a population adopt it, cannot be bettered by an alternative strategy (Smith & Price, 1973). Thus, the behavior of a large group of individuals signals highly valuable information about the environment. Since individual decisions are continuously tested by natural selection, the majority of individuals would only adapt the same behavioral strategy if it is advantageous. Therefore, the only strategy that persists will be one that, once evolved, cannot be bettered by any deviant individual. In evolution, the best strategy for an individual depends on the most popular behavior strategy in the population (Dawkins, 1976). Moreover, selection will penalize deviation from it. From an evolutionary perspective, a deviation from the behavior of the majority indicates a highly probable mistake. Taken together, the monitoring of deviations from the normative (majority) behavior could be deeply integrated into our neuronal performance-monitoring mechanisms.

s0030

A General Neurobiological Mechanism of Social Influence

p0150

Fast and efficient behavioral adjustments in a volatile environment are essential for the fitness of the organism.

Unsurprisingly, natural selection favors a simple and efficient neuronal reinforcement learning mechanism that assigns a subjective expectation to each choice option that is updated on trial-by-trial basis (Schultz et al., 1997). Learning from the social environment could create an additional selection pressure for the evolution of the neuronal mechanism-monitoring behavior of others (Dunbar, 2003). Many previous psychological studies have shown that social influence can share the same mechanisms with nonsocial learning (Heyes, 2012). The review of the recent neuroimaging studies further supports this conclusion and suggests that the ventral striatum and pMFC continuously update subjective values based on a comparison of their own outcomes and the behavior of others.

Au17

Au18

Further studies are clearly needed to clarify the role of other brain regions in social influence, such as the ventral MFC (Chua et al., 2009; Falk et al., 2013; Zak et al., 2010), the insular cortex (Berns et al., 2010; Huber, Klucharev, & Rieskamp, in press), and the precuneus (Falk et al., 2013). Much research remains to be done to reveal the fundamental neural mechanisms of social influence. We need to further study the nature of individual differences in conformity, check the similarity of the neural mechanisms underlying negative and positive reinforcement by social norms, and study developmental changes in conformity and many other aspects of social influence. Nevertheless, the current studies of the neural mechanism of social influence have started to uncover the mystery of our strong tendency to change our behavior so that it falls in line with the behavior of others.

p0155

Au19

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See also: **Social:** Social Rewards (00145); Observational Fear Learning (00168); Social Cognition During Social Interactions (00172); Social Decision-Making (00185); Attitudes (00186); Attitude Change & Cognitive Consistency (00188); **Anatomy & Physiology:** Mapping Cingulate Structure/function Subregions (00230); **Cognitive:** Reinforcement Learning (00257); Value Representation (00258).

References

Au22

- Ajzen, I., & Fishbein, M. (1980). *Understanding attitudes and predicting social behavior*. Englewood Cliffs, NJ: Prentice-Hall.
- Asch, S. (1951). Effects of group pressure upon the modification and distortion of judgments. In H. Guetzkow (Ed.), *Groups, leadership and men research in human Relations* (pp. 177–190). Pittsburgh, PA: Carnegie Press.
- Behrens, T. E. J., Hunt, L. T., Woolrich, M. W., & Rushworth, M. F. S. (2008). Associative learning of social value. *Nature*, *456*, 245–249.
- Berns, G. S., Capra, C. M., Moore, S., & Noussair, C. (2010). Neural mechanisms of the influence of popularity on adolescent ratings of music. *NeuroImage*, *49*, 2687–2696.
- Berns, G. S., Chappelow, J., Zink, C. F., Pagnoni, G., Martin-Skurski, M. E., & Richards, J. (2005). Neurobiological correlates of social conformity and independence during mental rotation. *Biological Psychiatry*, *58*, 245–253.
- Biele, G., Rieskamp, J., Krugel, L. K., & Heekeren, H. (2011). The neural basis of following advice. *PLoS Biology*, *9*, e1001089.

Bryan, J. H., & Test, M. A. J. (1967). Models and helping: Naturalistic studies in aiding behavior. *Journal of Personality and Social Psychology*, 6, 400–407.

Burke, C. J., Tobler, P. N., Baddeley, M., & Schultz, W. (2010). Neural mechanisms of observational learning. *Proceedings of the National Academy of Sciences of the United States of America*, 107, 14431–14436.

Campbell-Meiklejohn, D., Bach, D., Roepstorff, A., Dolan, R., & Frith, C. (2010). How the opinion of others affects our valuation of objects. *Current Biology*, 20, 1165–1170.

Campbell-Meiklejohn, D. K., Simonsen, A., Jensen, M., Wohlert, V., Gjerløff, T., Scheel-Kruger, J., et al. (2012). Modulation of social influence by methylphenidate. *Neuropsychopharmacology*, 37(6), 1517–1525.

Carelli, R. M. (2002). The nucleus accumbens and reward: Neurophysiological investigations in behaving animals. *Behavioral and Cognitive Neuroscience Reviews*, 1(4), 281–296.

Chase, H. W., Swainson, R., Durham, L., Benham, L., & Cools, R. (2011). Feedback-related negativity codes prediction error but not behavioral adjustment during probabilistic reversal learning. *Journal of Cognitive Neuroscience*, 23, 936–946.

Chen, J., Wu, Y., Tong, G., Guan, X., & Zhou, X. (2012). ERP correlates of social conformity in a line judgment task. *BMC Neuroscience*, 13, 43.

Chib, V. S., Rangel, A., Shimojo, S., & O'Doherty, J. P. (2009). Evidence for a common representation of decision values for dissimilar goods in human ventromedial prefrontal cortex. *Journal of Neuroscience*, 29(39), 12315–12320.

Chua, H. F., Liberzon, I., Welsh, R. C., & Strecher, V. J. (2009). Neural correlates of message tailoring and self-relatedness in smoking cessation programming. *Biological Psychiatry*, 65, 165–168.

Cialdini, R. B., & Goldstein, N. J. (2004). Social influence: Compliance and conformity. *Annual Review of Psychology*, 55, 591–621.

Cohen, M. X., & Ranganath, C. (2007). Reinforcement learning signals predict future decisions. *Journal of Neuroscience*, 27, 371–378.

Dawkins, R. (1976). *The selfish gene*. New York: Oxford University Press.

di Pellegrino, G., Ciaramelli, E., & Ladavas, E. (2007). The regulation of cognitive control following rostral anterior cingulate cortex lesion in humans. *Journal of Cognitive Neuroscience*, 19, 275–286.

Dunbar, R. I. M. (2003). The social brain: Mind, language, and society in evolutionary perspective. *Annual Review of Anthropology*, 32, 163–181.

Edelson, M., Sharot, T., Dolan, R. J., & Dudai, Y. (2011). Following the crowd: Brain substrates of social conformity. *NeuroImage*, 54, 100–108.

Falk, E. B., Berkman, E. T., Whalen, D., & Lieberman, M. D. (2011). Neural activity during health messaging predicts reductions in smoking above and beyond self-report. *Health Psychol*, 30, 177–185.

Falk, E. B., Morelli, S. A., Welborn, B. L., Dambacher, K., & Lieberman, M. D. (2013). Creating buzz: The neural correlates of effective message propagation. *Psychological Science*, 24, 995–1003. doi:10.1177/0956797612459567

Falk, E. B., O'Doherty, J., & Lieberman, M. D. (2012). Neural correlates of social influence. *NeuroImage*, 60, 313–321. doi:10.1016/j.neuroimage.2012.03.061

Fields, H. L., Hjelmstad, G. O., Margolis, E. B., & Nicola, S. M. (2007). Ventral tegmental area neurons in learned appetitive behavior and positive reinforcement. *Annual Review of Neuroscience*, 30, 289–316.

Gehring, W. J., & Willoughby, A. R. (2002). The medial frontal cortex and the rapid processing of monetary gains and losses. *Science*, 295, 2279–2282.

Groenewegen, H. J., Room, P., Witter, M. P., & Lohman, A. H. (1982). Cortical afferents of the nucleus accumbens in the cat, studied with anterograde and retrograde transport techniques. *Neuroscience*, 7, 977–996.

Hauber, W., & Sommer, S. (2009). Prefrontostriatal circuitry regulates effort-related decision making. *Cerebral Cortex*, 19, 2240–2247.

Heider, F. (1958). *The psychology of interpersonal relations*. New York: Wiley.

Heyes, C. (2012). What's social about social learning? *Journal of Comparative Psychology*, 126, 193–202.

Holroyd, C. B., & Coles, M. G. (2002). The neural basis of human error processing: Reinforcement learning, dopamine, and the error-related negativity. *Psychological Review*, 109, 679–709.

Klucharev, V., & Rieckmann, J. (in press). Neural correlates of informational cascades: Brain mechanisms of social influence on belief updating. *SCAN*.

Izuma, K. (2013). The neural basis of social influence and attitude change. *Current Opinion in Neurobiology*, 23(3), 456–462.

Izuma, K., & Adolphs, R. (2013). Social manipulation of preference in the human brain. *Neuron*, 78(3), 563–573.

Kenrick, D. T., Neuberg, S. L., & Cialdini, R. B. (2004). *Social psychology: Unraveling the mystery* (3rd ed.). Allyn & Bacon.

Kerns, J. G., Cohen, J. D., MacDonald, A. W., 3rd, Cho, R. Y., Stenger, V. A., & Carter, C. S. (2004). Anterior cingulate conflict monitoring and adjustments in control. *Science*, 303, 1023–1026.

Kim, B. R., Liss, A., Rao, M., Singer, Z., & Compton, R. J. (2012). Social deviance activates the brain's error-monitoring system. *Cognitive, Affective, & Behavioral Neuroscience*, 12(1), 65–73.

Klucharev, V., Munneke, M. A., Smidts, A., & Fernandez, G. (2011). Downregulation of the posterior medial frontal cortex prevents social conformity. *Journal of Neuroscience*, 31, 11934–11940.

Klucharev, V., Smidts, A., & Fernandez, G. (2008). Brain mechanisms of persuasion: How 'expert power' modulates memory and attitudes. *Social Cognitive and Affective Neuroscience*, 3, 353–366.

Knutson, B., & Wimmer, G. E. (2007). Splitting the difference: How does the brain code reward episodes? *Annals of the New York Academy of Sciences*, 1104, 54–69.

Matsumoto, M., Matsumoto, K., Abe, H., & Tanaka, K. (2007). Medial prefrontal cell activity signaling prediction errors of action values. *Nature Neuroscience*, 10, 647–656.

Miltner, W. H. R., Braun, C. H., & Coles, M. G. H. (1997). Event-related brain potentials following incorrect feedback in a time-estimation task: Evidence for a "generic" neural system for error detection. *Journal of Cognitive Neuroscience*, 9, 788–798.

Montague, P. R., & Lohrenz, T. (2007). To detect and correct: Norm violations and their enforcement. *Neuron*, 56, 14–18.

Nieuwenhuis, S., Holroyd, C. B., Mol, N., & Coles, M. G. (2004). Reinforcement-related brain potentials from medial frontal cortex: Origins and functional significance. *Neuroscience and Biobehavioral Reviews*, 28, 441–448.

Nieuwenhuis, S., Ridderinkhof, K. R., Blom, J., Band, G. P., & Kok, A. (2001). Error-related brain potentials are differentially related to awareness of response errors: Evidence from an antisaccade task. *Psychophysiology*, 38, 752–760.

Nieuwenhuis, S., Schweizer, T. S., Mars, R. B., Botvinick, M. M., & Hajcak, G. (2007). Error-likelihood prediction in the medial frontal cortex: A critical evaluation. *Cerebral Cortex*, 17, 1570–1581.

O'Doherty, J., Critchley, H., Deichmann, R., & Dolan, R. J. (2003). Dissociating value of outcome from behavioral control in human orbital and ventral prefrontal cortex. *Journal of Neuroscience*, 23, 7931–7939.

Orlitzky, D. J. (2002). *Persuasion. Theory and research*. Newbury Park, CA: Sage.

Ranson, J. A., Willoughby, P. J., Robbins, T. W., & Everitt, B. J. (2000). Disconnection of the anterior cingulate cortex and nucleus accumbens core impairs Pavlovian approach behavior: Further evidence for limbic cortical-ventral striatopallidal systems. *Behavioral Neuroscience*, 114, 42–63.

Raafat, R. M., Chater, N., & Frith, C. (2009). Herding in humans. *Trends in Cognitive Sciences*, 13, 420–428.

Rescorla, R. A., & Wagner, A. R. (1972). A theory of Pavlovian conditioning: The effectiveness of reinforcement and nonreinforcement. In W. F. (Eds.) *Classical conditioning II: Current research and applications* (pp. 67–90). New York: Appleton-Century-Crofts.

Schultz, W. (2006). Behavioral theories and the neurophysiology of learning. *Annual Review of Psychology*, 57, 87–115.

Smith, M. J., & Price, G. R. (1973). The logic of animal conflict. *Nature*, 246(5427), 15–18.

Stallen, M., Smidts, A., Rijkema, M., Smit, G., & Klucharev, V. (2010). Celebrities and shoes on the female brain. The neural correlates of product evaluation in the context of fame. *Journal of Economic Psychology*, 31(5), 802–811.

van Schie, H. T., Mars, R. B., Coles, M. G. H., & Bekkering, H. (2004). Modulation of activity in medial frontal and motor cortices during error observation. *Nature Neuroscience*, 7, 549–554.

Zaki, J., Schirmer, J., & Mitchell, J. P. (2011). Social influence modulates the neural computation of value. *Psychological Science*, 22, 894–900.

Kesebir S. The superorganism account of human sociality: how and when human groups are like beehives. *Pers Soc Psychol Rev*. 2012 Aug;16(3), 233-261. doi: 10.1177/1088868311430834. Epub 2011 Dec 27.

Klucharev V., Hytonen K., Rijkema M., Smidts A. and Fernandez G. (2009) Reinforcement learning signal predicts social conformity. *Neuron*, 61, 140-151.

Nieuwenhuis, S., Slagter, H.A., von Geusau, N.J.A., Heslenfeld, D.J., Holroyd, C.B., (2005). Knowing good from bad: differential activation of human cortical areas by positive and negative outcomes. *The European Journal of Neuroscience* 21, 3161-3168.

Rolls ET, Grabenhorst F. (2008) The orbitofrontal cortex and beyond: from affect to decision-making. *Prog Neurobiol*. Nov;86(3), 216-244.

Schultz W, Dayan P, Montague PR. (1997) A neural substrate of prediction and reward. *Science*. 275(5306), 1593-9.

Relevant Websites

<http://cn.asc.upenn.edu/> – Communication Neuroscience Lab of the University of Pennsylvania.
<http://interactingminds.au.dk/about-the-centre/> – The Interacting Minds Centre for Study of Cognition, Communication and Choice.

Shestakova A, Rieskamp J, Tugin S, Ossadtschi A, Krutitskaya J, Klucharev V (2013) Electrophysiological precursors of social conformity. *Soc Cogn Affect Neurosci*. 8(7), 756-763.