Neural Responses to Taxation and Voluntary Giving Reveal Motives for Charitable Donations
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The scaffold protein Dvl was previously thought to act downstream of LRP6 because dsh overexpression activates β-catenin signaling in Drosophila LRP6 (arrow) mutants (23) and because the constitutively active D62-Arrow fusion protein is inactive in dsh mutants (24). The explanation for this discrepancy may be that overexpressing Dsh/Dvl leads to artificial sequestration of Axin or that the protein has multiple functions in the Wnt pathway.

Taken together, the results suggest that Dvl-mediated co-agonization triggers LRP6 phosphorylation by CK1γ. In this model (Fig. 4D), upon Wnt signaling Dvl aggregates form at the plasma membrane, where they co-cluster LRP6 with other pathway components including Fz, Axin, and GSK3β, in a “LRP6-signalsome.” The role of Wnt would be to bridge LRP6 and Fz (25, 5), which copolymerize on a Dvl platform. Clustering of LRP6 then provides a high local receptor concentration that triggers phosphorylation by CK1γ and Axin recruitment.

Predictions of this model are as follows: (i) artificial oligomerization of LRP6 should activate the receptor and (ii) oligomerized LRP6 should signal independent of Dvl. Indeed, forced oligomerization of LRP6 using a synthetic multimerizer is sufficient to induce Wnt signaling, and this oligomerization bypasses the need for Dvl (25). (iii) Constitutive active LRP6 should signal independently of Dvl because its self-aggregation should bypass the need for Dvl polymers. This is also the case as shown in reporter assays with Dvl siRNA knockdown (fig. S5, B and C), which supports previous findings (26, 25). (iv) If LRP6 aggregation is a prerequisite for phosphorylation by CK1γ rather than its consequence, LRP6 aggregates should form even when the kinase is blocked. This is the case: Nonphosphorylated LRP6 aggregates were observed in response to Wnt treatment in cells transfected with dominant-negative CK1γ (fig. 4C). The model of LRP6-signalsomes not only provides a mechanism for Wnt signal transduction but may also be relevant for the understanding of intracellular transport of maternal Wnt determinants in the fertilized Xenopus egg (27).

References and Notes
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28. We thank R. Pepperkok for support in the EMBL Advanced Light Microscopy Facility; the Nikon Imaging Center at the University of Heidelberg and M. Boutros and D. Ingelfinger for help with siRNA experiments; A. Glinka for advice; N. Maltry for technical help; and J. Axelrod, A. Helenius, J. Nathans, R. Nusse, T. Schwarz-Romond, and M. Semenov for reagents. This work was supported by the European Union (Endotrack) and the Deutsche Forschungsgemeinschaft.

Supporting Online Material
www.sciencemag.org/cgi/content/full/316/5831/1619/DC1
Materials and Methods
Figs. S1 to S5
Movie S1

Neural Responses to Taxation and Voluntary Giving Reveal Motives for Charitable Donations

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Civil societies function because people pay taxes and make charitable contributions to provide public goods. One possible motive for charitable contributions, called “pure altruism,” is satisfied by increases in the public good no matter the source or intent. Another possible motive, “warm glow,” is only fulfilled by an individual’s own voluntary donations. Consistent with pure altruism, we find that even mandatory, tax-like transfers to a charity elicit neural activity in areas linked to reward processing. Moreover, neural responses to the charity’s financial gains predict voluntary giving. However, consistent with warm glow, neural activity further increases when people make transfers voluntarily. Both pure altruism and warm-glow motives appear to determine the hedonic consequences of financial transfers to the public good.

Every society needs public goods, but the mechanisms used to fund them vary. For example, taxation and government spending are lower in the United States than in most European countries, but philanthropy is higher (1). To economists, this charitable giving is a puzzle: Money is a good, so why are people willing to give some satisfaction even when public goods are supplied through mandatory taxation, because, by this account, people care only about how much of the public good is provided and not about the process by which the transfer occurs. A second possible motive for charitable giving is the sense of agency associated with the act of voluntary giving. This reward from giving has been termed “warm glow” (3, 4). If givers were driven exclusively by the warm-glow motive, they should derive satisfaction from making a voluntary gift, rather than from the increase in the level of the public good itself. On the other hand, taxation should not produce a warm glow, because paying taxes typically does not involve a voluntary choice.

The distinction between pure altruism and warm-glow motives for giving is important for several reasons. First, if giving is motivated by pure altruism, tax-funded government expenditures to provide a public good will reduce private giving, potentially dollar for dollar, as people cut their voluntary contributions in response to these higher taxes (4). There should be no similar effect with warm-glow givers, as their benefit derives from the amount of their gift. Second, a warm-glow motive for altruism provides an argument in favor of policies that encourage voluntary giving, because the warm-glow benefit provides a reward to the giver that exceeds the benefit from paying an equivalent amount in taxes (6).

Neural evidence may help clarify the relative importance of pure altruism and warm-glow motives for charitable giving. Although there is
considerable evidence linking neural activity in the ventral striatum and the insulae to the processing of concrete rewards such as money, food, and drugs, less is known about how the brain processes more abstract rewards such as those often provided by public goods. For money, activity in the ventral striatum increases as people anticipate increases in payoffs and when they receive unexpected increases in payoffs (7, 8). Neural responses in the ventral striatum and insulae to information about products and their prices also predict purchase decisions (9). This work supports the theory that these areas provide information on the relative rewards of different outcomes, which serve as an input to decisions about consumption and tradeoffs regarding risk and money (10). Other studies have shown that activity in the ventral striatum and the insulae is correlated with more abstract rewards, including social rewards such as punishing unfair players in sharing games (11), voluntary contributions to charities (12, 13), and decisions to trust others (14, 15). These results motivate our focus on the ventral striatum and the insulae.

To test for the pure altruism and warm-glow motives, we used functional magnetic resonance imaging while subjects played a dictator game. Subjects received $100 and then made decisions about whether or not to give money to a local food bank. They also observed mandatory, tax-like transfers of their money to the food bank (Fig. 1, A and B) (16). The behavioral results in this experiment are consistent with economic theory and are similar to those reported in earlier economic experiments (17–19). As shown in Fig. 2A, increases in the amounts going to the charity and decreases in the cost to the giver both increased the likelihood that a voluntary transfer was accepted. Self-reported satisfaction with the transaction followed the same pattern in both the voluntary and the mandatory conditions (Fig. 2B).

To investigate the neural activity associated with pure altruism, we used data from the mandatory treatments, which involved exogenous changes in subject and charity payoffs. Contrasts of parameter estimates (Fig. 3) show that activation in very similar areas of the ventral striatum increased with the monetary payoff to both the subject and to the charity. Regression analyses to explain activation data extracted from anatomical regions of interest (ROIs) show the same result (table S4) (16). This is the first evidence we know of demonstrating that mandatory taxation for a good cause can produce activation in specific brain areas that have been tied to concrete, individualistic rewards.

The pure altruism model predicts that people who highly value increases in the charity’s payoff, relative to the value they place on getting money for themselves, will be more likely to give. The evidence economists have typically used to support this model has been indirect: Relative values have been inferred from observed decisions (20). Our experiment allowed us to observe brain activation, in areas known to respond to rewards, as we varied the money the subject received and the money the charity received. This provides a direct test of the model: Do across-subject differences in neural responses to subject and charity payoffs predict who is more likely to give to the charity?

We are able to address this question out of treatment by using neural responses in those “pure” mandatory conditions where only the subject or only the charity got money (orange and green cells, respectively, in Fig. 1B). These responses potentially serve as an indicator of how much subjects valued money for themselves and for the charity. In fact, regression coefficients show that subjects with larger activation responses to money for themselves were less likely to give to the charity (black columns in Fig. 4A), and subjects with larger activation responses to money for the charity were more likely to give (gray columns in Fig. 4A). To illustrate this rela-

**Fig. 1.** (A) Study protocol. We scanned 19 females using functional magnetic resonance imaging (fMRI) while they were presented with transfers that affected their own account (starting amount, $100) and the account of a local charity. Half the transfers were mandatory, to resemble taxation; the other half were voluntary. We explained that the experimenters would not know their choices and that one mandatory and one voluntary transfer would be randomly chosen and implemented after the experiment. Events for each trial occurred as presented in the time line, details are in the supporting online material (26). After a 1-s fixation dot, the screen revealed whether this trial’s transfer was mandatory or voluntary, as well as the dollar amount change to the accounts of the subject and the charity. After 9 s, two vertically aligned labels were added in the lower portion of the screen, specifying the vertically aligned buttons on a response box. For mandatory transfers, one of the labels read “acknowledge” and the other “invalid button.” For voluntary transfers, one of the labels read “accept” and the other “reject.” Label positions varied randomly from trial to trial. Immediately after the subject’s response, a four-point satisfaction rating scale was shown, to which subjects responded by pressing one of four laterally oriented keys on the button box. The rating scale disappeared after 6 s, and there was a blank screen for an intertrial period that was randomly jittered between 6, 7, and 8 s. (B) Study design. The cells show the dollar transfers. Each design cell was implemented three times as a mandatory transfer and three times as a voluntary decision. Orange cells indicate pure gains to the subject; green cells indicate pure gains to the charity. These pure-gain design cells from the mandatory condition were used to predict voluntary giving in the purple cells, where there was a tradeoff between the subject and the charity (see Fig. 4, A and B).

**Fig. 2.** (A) Subjects’ choices during voluntary transfers as a function of payoffs to the subject and the charity. Many transfers that were costly to the subject but benefited the charity were accepted, and the rate of acceptance increased as the cost of making a given transfer declined. (B) Subjective satisfaction ratings as a function of payoffs to the subject and the charity, as well as the voluntary-mandatory factor. Subjective satisfaction increased as transfers increased and costs decreased and was higher in the voluntary (solid lines) than in the mandatory conditions (dashed lines).

**Fig. 3.** Neural response in the ventral striatum to mandatory payoffs for the subject (yellow), the charity (blue), and both (green).
Fig. 4. (A) Predicting giving from activations in mandatory “pure-gain” conditions. We created measures of neural activation in response to “pure subject gain” and “pure charity gain” by averaging activation from the mandatory conditions where the subject received money at no cost to the charity and where the charity received money at no cost to the subject (orange and green cells, respectively; in Fig. 1B). We used these two sets of activations as independent predictors of the average acceptance rate in the nine design cells involving a tradeoff (purple cells in Fig. 1B). The figure shows standardized probit regression coefficients from models including subject and charity stakes as control variables and neural response to pure subject gains and pure charity gains as independent predictors. The dashed lines indicate \( P = 0.05 \) significance. Higher response to pure subject gain was consistently associated with less giving. Higher response to pure charity gains was consistently associated with more giving. Coefficients for individual predictors were reliable in seven out of 12 cases. (B) Differences in activation predict giving. As an overall measure, we averaged the neural activation measures across all six brain areas and computed the difference between neural responses to the charity’s pure gains and the neural responses to the subject’s pure gains (orange and green cells in Fig. 2B). Giving increased as the neural response to pure charity gains outweighed the neural response to pure subject gains (\( R^2 = 27\%, P = 0.02 \)).
last, public goods by their very nature are seldom traded in markets, and so we cannot observe the prices people will pay and then use these to measure value. The finding that neural activity predicts voluntary donations suggests that such activity could eventually help measure values and determine optimal levels of public goods.

References and Notes

16. Materials and methods are available as supporting material in Science Online.
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Supporting Online Material

www.sciencemag.org/cgi/content/full/316/5831/1622/DC1
Materials and Methods
Fig. S1
Tables S1 to S7
References

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Sequence Finishing and Mapping of Drosophila melanogaster Heterochromatin

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Genome sequences for most metazoans and plants are incomplete because of the presence of repeated DNA in the heterochromatin. The heterochromatic regions of Drosophila melanogaster contain 20 million bases (Mb) of sequence amenable to mapping, sequence assembly, and finishing. We describe the generation of 15 Mb of finished or improved heterochromatic sequence with the use of available clone resources and assembly methods. We also constructed a bacterial artificial chromosome-based sequence library that spans 13 Mb of the pericentric heterochromatin and a cytogenetic map that positions 11 Mb in specific chromosomal locations. We have approached a complete assembly and mapping of the nonsatellite component of Drosophila heterochromatin. The strategy we describe is also applicable to generating substantially more information about heterochromatin in other species, including humans.

Heterochromatin is a major component of metazoan and plant genomes (e.g., ~20% of the human genome) that regulates chromosome segregation, nuclear organization, and gene expression (1–4). A thorough description of the sequence and organization of heterochromatin is necessary for understanding the essential functions encoded within this region of the genome. However, difficulties in cloning, mapping, and assembling regions rich in repetitive elements have hindered the genomic analysis of heterochromatin (5–7). The fruit fly Drosophila melanogaster is a model for heterochromatin studies. About one-third of the genome is considered heterochromatic and is concentrated in the pericentric and telomeric regions of the chromosomes (X, 2, 3, 4, and Y) (5, 8). The heterochromatin contains tandemly repeated simple sequences (including satellite DNA) (9), middle repetitive elements (such as transposable elements [TEs] and ribosomal DNA), and some single-copy DNA (10).

The whole-genome shotgun sequence (WGS3) was the foundation for finishing and mapping heterochromatic sequences and for elucidating the organization and composition of the nonsatellite DNA in Drosophila heterochromatin (5, 6). WGS3 is an excellent assembly of the Drosophila euchromatic sequence, but it has lower contiguity and quality in the repeat-rich heterochromatin. We undertook a retrospective analysis of these WGS3 scaffolds (11). Moderately repetitive sequences, such as transposable elements, are well represented in WGS clones and sequence reads, but they tend to be assembled into shorter scaffolds with many gaps and low-quality regions because of the difficulty of accurately assigning data to a specific copy of a repeat. The typical WGS heterochromatic scaffold is smaller [for scaffolds mapped to an arm, N50 ranged from 4 to 35 kb (11)] than a typical WGS euchromatic scaffold (N50 = 13.9 Mb) (5). Relative to the euchromatic scaffolds, the WGS3 heterochromatic scaffolds have 5.8 times as many sequence gaps per Mb, as well as lower sequence quality.

To produce the Release 5 sequence, we identified a set of 10-kb genomic clones from a library representing 15× coverage by paired end reads (mate pairs) and used this set as templates to fill small gaps and improve low-quality regions (12). Higher-level sequence assembly into Mb-sized linked scaffolds used relationships determined from bacterial artificial chromosome (BAC)–based sequence tag site (STS) physical mapping (see below) and BAC end sequences. In addition to the WGS data, we incorporated data from 30 BACs (3.4 Mb; 15 BACs finished since Release 3) that were originally sequenced as part of the euchromatin sequencing effort (5, 10).

Sequence finishing resulted in fewer gaps, longer scaffolds, and higher-quality sequence relative to WGS3 (fig. S1). About 15 Mb of this sequence has been finished or improved, and 50% of the sequence is now in scaffolds greater than 378 kb (N50). Table 1 summarizes the Release 5 sequence statistics by chromosome arm. Improved sequence was generated for 145 WGS3 scaffolds, and a set of 90 new scaffolds were produced by joining or filling 694 gaps of previously unknown size between WGS3 scaffolds. The relationships between the initial WGS scaffolds and the Release 5 scaffolds can be complex (Fig. 1 and figs. S2 to S7); for example, there were eight cases in which small scaffolds were used to fill gaps within larger scaffolds, and two scaffolds whose gaps interdigitated. As expected, the sequence consists largely of nests of frag-