Compartments revealed in food-web structure

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Compartments[1] in food webs are subgroups of taxa in which many strong interactions occur within the subgroups and few weak interactions occur between the subgroups[2]. Theoretically, compartments increase the stability in networks[1–5], such as food webs. Compartments have been difficult to detect in empirical food webs because of incompatible approaches[6–9] or insufficient methodological rigour[8,10,11]. Here we show that a method for detecting compartments from the social networking science[12–14] identified significant compartments in three of five complex, empirical food webs. Detection of compartments was influenced by food web resolution, such as interactions with weights. Because the method identifies compartmental boundaries in which interactions are concentrated, it is compatible with the definition of compartments. The method is rigorous because it maximizes an explicit function, identifies the number of non-overlapping compartments, assigns membership to compartments, and tests the statistical significance of the results[12–14]. A graphical presentation[14] reveals systemic relationships and taxa-specific positions as structured by compartments. From this graphic, we explore two scenarios of disturbance to develop a hypothesis for testing how compartmentalized interactions increase stability in food webs[15–17].

Similarity between human social networks and food webs has recently been noted through exchanges between ecologists and sociologists[18,19]. In the social sciences, cohesive subgroups in human communities have been an important concept since the 1950s, when it was proposed that social systems were more efficient and durable when composed of subgroups in which interactions were concentrated[3,20,21]. The concept of cohesive subgroups has had strong theoretical support, but the methodologies needed to apply the concept to communities were lacking[12,13]. This is also the case for food-web compartments in ecology, wherein methods for identifying compartments have often emphasized the similarity of prey and predators between taxa[6–9], which results in little direct interaction or carbon exchange within compartments.

Here we use a recently developed social network method[12,14] for identifying cohesive subgroups to detect compartments in empirical food webs. The method identifies compartments in which interactions are concentrated, thus conserving the flow of energy and organic material, for example, within compartments, just as information and influence flow primarily within human subgroups in which interactions are concentrated. Although the algorithm identifies compartments in which interactions are concentrated, interactions are not exclusively confined within compartments. Thus there are critical cross-compartment interactions that integrate the compartments into a food web[1], just as interactions between people in different subgroups sustain social systems and societies[3,20,21].

Crucial to the network method is the criterion defining the concentration of interactions within compartments, where an interaction is predator taxon i consuming prey taxon i'. The criterion is the increase in the odds of an interaction occurring (as opposed to not occurring) given that two taxa are in the same compartment as opposed to in different compartments. This odds ratio corresponds to $[(A\times D)/(B\times C)]$ as defined in Table 1 and can be interpreted as a comparison of density of interactions within versus between compartments and is thus associated with key parameters for social network models[12]. The statistical significance of the odds ratio is determined by Monte Carlo simulations (see Methods). In the food-web literature[22], density is analogous to interactive connectance (IC), with overall IC defined by $[(B+D)/(A+B+C+D)]$ and interpreted as the proportion of realized interactions out of all possible interactions.

The algorithm we employed has four features[12–14] that are crucial for our application[6,23]. First, taxa are assigned to non-overlapping compartments as a result of the odds ratio being a flexible criterion[12–14]. Thus, the assignment of each taxon contributes to the concentration of interactions within all of the compartments of the food web[12]. Second, the algorithm generally does not require a priori specification of the number of compartments. This feature removes a key subjective decision from the procedure and assists in simulating a sampling distribution for the odds ratio. Third, the algorithm was calibrated by applying it to extensive simulated data with known compartment assignments[12,13]. Fourth, compartment boundaries can be embedded in a graphical presentation of the food web[13], thus facilitating the interpretation of the roles of compartments and their taxa within food webs. None of the previous methodologies in either social networks[11–14] or ecology[6–11] have all four of these important features.

We applied this method to five food webs: Ythan Estuary[24], Little Rock Lake[22,25], St Martin Island[26], Chesapeake Bay[27,28] and a cypress wetland (See Supplementary Information A). Seventeen separate versions of these food webs with various levels of aggregation of taxa, weight of interactions and season were considered. Seven of them yielded odds ratios that were statistically significantly greater than would be expected by chance alone (Table 2; $\alpha = 0.05$). Six of these would still be statistically significant when adjusting for the number of tests by using a Bonferroni correction of α. As we expected, IC within compartments was higher and IC between compartments was lower than the overall IC (by factors of 1.9 to 3.5 and 0.003 to 0.27 respectively). The algorithm did not detect compartments in St Martin Island, a narrow food web focused on two lizard species and not likely to have compartments, but did detect compartments in broader food webs (for example, Chesapeake Bay). This is consistent with our claim that the method is able to detect the presence or absence of compartments with reasonable accuracy.

The resolution of a food web can affect the detection of compartments. We detected compartmentalization in only 1 of 14 less complex food webs originally analysed[6,8] (Supplementary Information B) as opposed to three of five more complex food webs presented here. No compartments were detected in the aggregated version of Little Rock Lake or in the unweighted versions of Chesapeake Bay and the cypress wetland, whereas compartments were detected in alternative versions. These inconsistencies suggest that ignoring weights when aggregating taxa decreases the number of analysed interactions and can obscure strong relationships that contribute to compartmentalization. Note that the range in weights for interactions in all of our food-web versions was at the upper limit for the method. Ideally, the range should be narrower (for example, from 1 to 100). A wide range in weights (for example, from 1 to 99,999) can result from high aggregation in the basal taxa and low aggregation in top predators, such as in our weighted food webs.

The graphical presentation (Fig. 1) shows the compartmental structure of the Chesapeake Bay food web with 45 taxa and weighted by interaction strength. Although the detail in this graphic seems complex[23], the image reveals an intuitive understanding of the food

Table 1 **Association between compartment membership and occurrence of interactions between taxa**

		Interaction occurring		
		No	Yes	
Compartment membership	Different	A	B	$n(n-1)-\Sigma_g n_g(n_g-1)$
	Same	C	D	$\Sigma_g n_g(n_g-1)$
		$n(n-1)-\Sigma_i\Sigma_{i'}X_{ii'}$	$\Sigma_i\Sigma_{i'}X_{ii'}$	$n(n-1)$

$X_{ii'}$ represents the presence (1) or absence (0) of an interaction between taxon i and taxon i', n the number of taxa in the food web, and n_g the number of taxa in compartment g. Interactions between predator taxon i and prey taxon i' can be weighted by integers from 0 to W_m, the maximum weight across all ii' interactions. Weights are included in the above table by multiplying $X_{ii'}$ by the weight assigned to the ii' interaction and by multiplying $n(n-1)$ and $\Sigma_g n_g(n_g-1)$ by W_m (ref. 13). A represents unrealized interactions between compartments, B realized interactions between compartments, C unrealized interactions within compartments, and D realized interactions within compartments.

web. Compartment A has 28 taxa, most of which would be considered pelagic (in the water column) and compartment B has 17 taxa that are primarily benthic (in sediments). Some taxa placements might seem counterintuitive when considering the physical component of habitat. For example, clams (27, 28 and 29) and oyster (30) physically reside in the benthos, like the clams (25 and 26) in compartment B. Our results demonstrate that the biotic habitat of 27, 28, 29 and 30 is in the pelagia because of their strong interactions with bacteria (3, 4 and 5) and ciliates (7, 8 and 9) in compartment A, which supports previous research[27]. Compartments should measure biotic habitat[8,10,11], and compartment membership from our other significant results (Supplementary Information C) lend additional support. At the system level, compartments A and B are linked through cross-compartment interactions. The few weak interactions indicate the level of isolation between the two compartments. The interactions that compartment B has with A are more evenly dispersed within its compartment, where 65% of its taxa interact with A. Conversely, only 30% of the taxa in compartment A interact with B and these interactions are concentrated within specific areas of A.

Placement of a taxon indicates its role within its compartment. For compartment B, taxa 2, 22 and 45 are centrally located, indicating their importance to compartmental interactions, particularly in comparison with those taxa around the periphery of compartment B, such as 21, 33 and 41. Central to compartment A is a food chain (1, 6 and 14). Of the 25 other taxa in A, 23 interact with one of these three taxa. Peripheral taxa placed near to another compartment relate more strongly to that compartment than peripheral taxa placed further away. For example, peripheral taxon 16 has two interactions within compartment A and interacts with taxa that only interact within A, so 16's position is far from B. Conversely, peripheral taxon 41 has one interaction within compartment B and one that goes to A, so its position within B is close to A. Taxon 36 has the role of a bridging taxon between compartments A and B, where most of the interactions between A and B are attributable to 36.

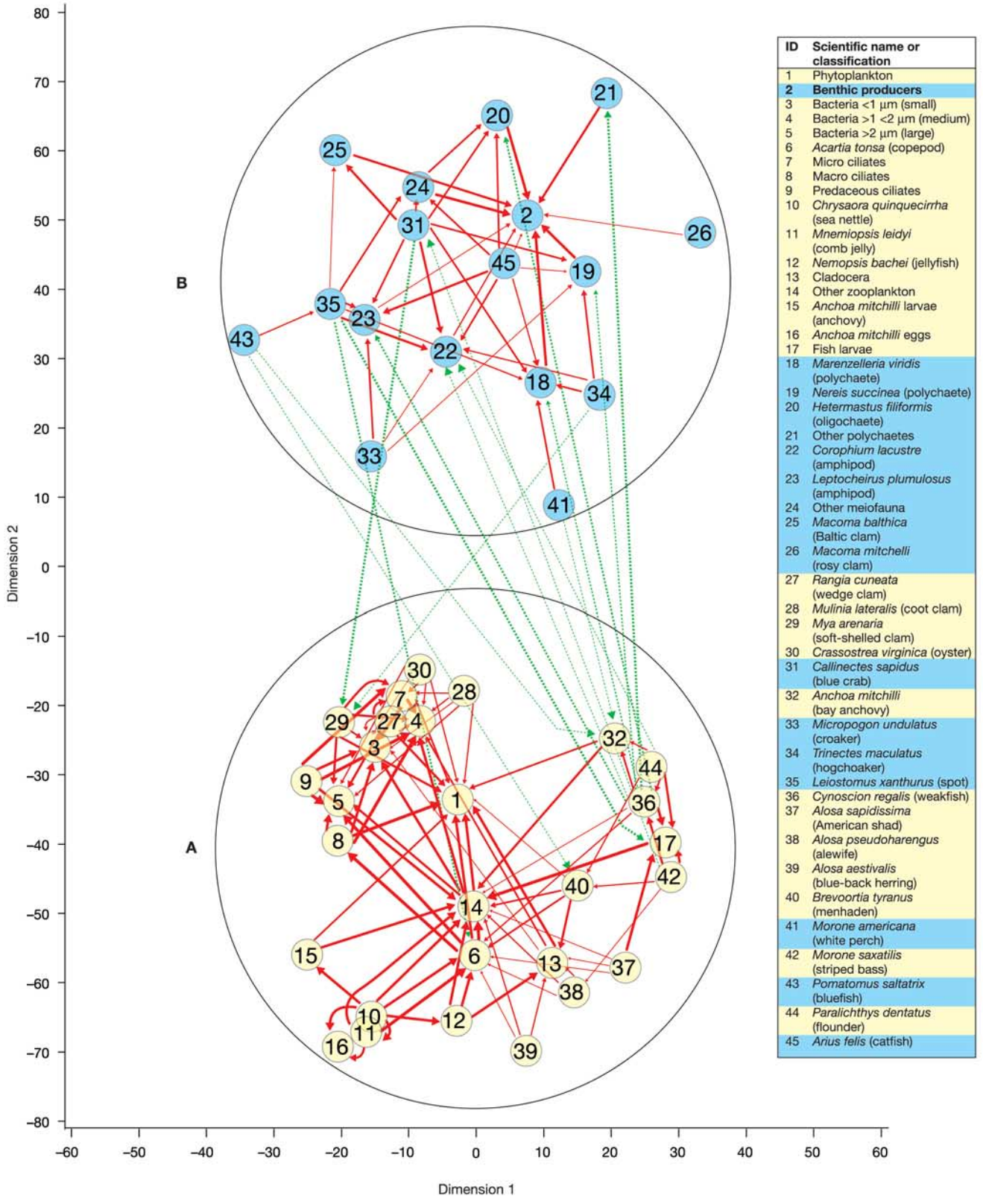
Because previous work relates compartments to stability[1–5], we developed a hypothesis of stability by simulating two disturbance scenarios on our food web in Fig. 1. The first removes weakfish (36), which could occur with overfishing. This disturbance[15] translates to a decrease in the number of taxa (−2% = taxa loss). Our overall IC, a variable of interest[15,17], was −1.5-fold the taxa loss. The IC within compartment A, where 36 was a member, was −3-fold the taxa loss, whereas the IC within B showed no change. Between IC was 18-fold the taxa loss because 36 was a dominant bridging taxon. In our second scenario we considered replacing *Acartia tonsa* (6), a central taxon in compartment A, with an invading zooplankton, a peripheral taxon, that preys only on large bacteria (5) and macrociliates (8) in A and is unpalatable to predators. This new invader reduces realized interactions (−5% = interaction loss). In response to this disturbance, the overall IC changed by the same percentage (1-fold the interaction loss, as expected), as did the IC within compartment A. The IC within compartment B was −0.3-fold the interaction loss and the between IC was 1.5-fold the interaction loss. Because the factoral change in IC values in relation to the disturbance index (taxa or interaction loss) indicates resistance[15], we propose that compartment B would be the most resistant and the exchange between A and B would be the least resistant to both disturbance events. That is, compartmentalization retains the impacts of a disturbance within a single compartment, minimizing impacts on other compartments and thus providing the stabilizing structure to food webs. This hypothesis is consistent with previous studies[16] that found that weak interactions buffer the effect of disturbances, demonstrated by compartment B's resistance to disturbances occurring in A.

An empirical test[29] of hypotheses such as ours requires longitudinal data for multiple food webs, compartmentalized and uncompartmentalized[1–5], that have undergone disturbance events[15].

Table 2 **Compartment analysis for five food webs**

Name	*n*	Weight of interaction	Odds ratio	*P*	Number of compartments	Overall IC	Within IC	Between IC
Ythan Estuary	134	None	4.19	≥0.999	3	0.033	–	–
Little Rock Lake	92	None	3.14	≥0.999	2	0.12	–	–
	181	None	10.04	≤0.001*	4	0.072	0.17	0.020
St Martin Island	44	None	4.20	≤0.907	5	0.11	–	–
	44	Frequency	28.93	≤0.803	6	0.0065	–	–
Chesapeake Bay	33	None	8.61	≤0.751	3	0.067	–	–
	33	Strength	642.55	≤0.001*	2	0.0029	0.0059	0.0000093
	33	Carbon	618.75	≤0.012*	2	0.0035	0.0071	0.000012
	45	None	9.63	≤0.200	4	0.069	–	–
	45	Strength	114.92	≤0.001*	2	0.0052	0.0099	0.000087
	45	Carbon	165.84	≤0.001*	3	0.0018	0.0044	0.000026
Cypress wetland								
Dry season	64	None	5.52	≤0.285	2	0.11	–	–
	64	Strength	11.93	≤0.918	3	0.0021	–	–
	64	Carbon	228.18	≤0.001*	5	0.00057	0.0020	0.0000088
Wet season	64	None	7.81	≤0.001	1	0.11	–	–
	64	Strength	12.34	≤0.910	4	0.0026	–	–
	64	Carbon	384.81	≤0.001*	3	0.00044	0.0013	0.0000033

See the text and Table 1 for the calculations of the odds ratio, overall IC and definitions of A, B, C and D. IC within compartments is calculated as D/(C+D), and IC between compartments is calculated as B/(A + B). Asterisk indicates significance at $\alpha = 0.05$.



ID	Scientific name or classification
1	Phytoplankton
2	**Benthic producers**
3	Bacteria <1 μm (small)
4	Bacteria >1 <2 μm (medium)
5	Bacteria >2 μm (large)
6	*Acartia tonsa* (copepod)
7	Micro ciliates
8	Macro ciliates
9	Predaceous ciliates
10	*Chrysaora quinquecirrha* (sea nettle)
11	*Mnemiopsis leidyi* (comb jelly)
12	*Nemopsis bachei* (jellyfish)
13	Cladocera
14	Other zooplankton
15	*Anchoa mitchilli* larvae (anchovy)
16	*Anchoa mitchilli* eggs
17	Fish larvae
18	*Marenzelleria viridis* (polychaete)
19	*Nereis succinea* (polychaete)
20	*Hetermastus filiformis* (oligochaete)
21	Other polychaetes
22	*Corophium lacustre* (amphipod)
23	*Leptocheirus plumulosus* (amphipod)
24	Other meiofauna
25	*Macoma balthica* (Baltic clam)
26	*Macoma mitchelli* (rosy clam)
27	*Rangia cuneata* (wedge clam)
28	*Mulinia lateralis* (coot clam)
29	*Mya arenaria* (soft-shelled clam)
30	*Crassostrea virginica* (oyster)
31	*Callinectes sapidus* (blue crab)
32	*Anchoa mitchilli* (bay anchovy)
33	*Micropogon undulatus* (croaker)
34	*Trinectes maculatus* (hogchoaker)
35	*Leiostomus xanthurus* (spot)
36	*Cynoscion regalis* (weakfish)
37	*Alosa sapidissima* (American shad)
38	*Alosa pseudoharengus* (alewife)
39	*Alosa aestivalis* (blue-back herring)
40	*Brevoortia tyranus* (menhaden)
41	*Morone americana* (white perch)
42	*Morone saxatilis* (striped bass)
43	*Pomatomus saltatrix* (bluefish)
44	*Paralichthys dentatus* (flounder)
45	*Arius felis* (catfish)

Figure 1 Graphical display of the results for the Chesapeake Bay food web with 45 taxa and weighted by interaction strength. Units are relative distances based on the inverse of the density of interactions. Within-compartment distances were decreased by a factor of 6.2 for aesthetic purposes. Circles indicate compartment boundaries and numbers identify taxa (yellow, within compartment A; blue, within compartment B). Arrows indicate interactions between taxa (solid red, within compartment; dashed green, between compartments; thickness indicates rank of associated interaction strength) and point from predator to prey.

The changes in variables of interest (for example, IC) should be assessed for stability properties, such as resistance[15]. Our results show that this method is a rigorous and effective way to analyse food-web structure and provide the initial steps in understanding the relationship between compartments and stability[1–5]. □

Methods

Interactions were weighted by interaction frequency, by carbon flow or by interaction strength. Interaction frequency was estimated as acts of predation per hectare per day[26]. Carbon flow from prey i' to predator i, $W_{ii'}$, was estimated as $\mathrm{g\,C\,m^{-2}\,yr^{-1}}$ (refs 27, 28). Interaction strength was the geometric mean of the interaction strengths between predator i and prey i' (ref. 30). The interaction strength of predator i on prey i' was measured as $-(W_{ii'}/B_i)$, where B_i is the biomass of predator i ($\mathrm{g\,C\,m^{-2}}$), and the interaction strength of prey i' on predator i was measured as $R_i(W_{ii'}/B_{i'})$, where $B_{i'}$ is the biomass of prey i' ($\mathrm{g\,C\,m^{-2}}$) and R_i is the production to consumption ratio of predator i (ref. 30). With weights, the definition of IC becomes the proportion of possible interactions, each with maximum weight, that are realized (with no cannibalistic interactions).

We used the software KliqueFinder[12] to identify compartments. Because KliqueFinder operates on an integer scale from 1 to 99,999 we modified the interactions for weighted versions of the food webs to fit the scale. The modifications had little or no effect on the results. To test whether the concentration of interactions within identified compartments was greater than what was likely to have occurred by chance alone, for each web we conducted Monte Carlo simulations. First, we randomly reassigned interactions, constraining the row marginal (sum of each row in a matrix) to be equal to the row marginal of the original food web, where rows represented predators and columns represented prey. We then applied KliqueFinder and recorded the odds ratio. We then repeated this process 1,000 times to obtain a sampling distribution against which we could compare the empirical odds ratio. Our constraints ensured that the simulated food webs had the same number of predators, the same number (and weight) of interactions associated with a predator, and the same total number (and weight) of realized interactions as the original food web. Basal taxa (taxa with no prey) did vary in simulations for some food web versions, which did change the overall IC from the original for some food webs but we found that there was little or no effect on the P values and no effect on statistical inference.

Although the range of calibrating simulations[12,14] (the third feature of the methodology) did not allow a direct assessment of the performance of the algorithm for our data (because of large n and weighted interactions), the algorithm typically performs well when there is evidence of compartments in non-weighted data[12]. Cannibalism and taxa that interacted with only one other taxon were dropped from the analysis when optimizing the odds ratio because these interactions do not add information to the relative assignments of taxa to compartments. Dropped taxa were added back to the food web for the calculations in Table 2.

Coordinates for the diagram in Fig. 1 were generated by employing multidimensional scaling within and between subgroups[13], and SAS proc gplot was used to generate the figure. Because of the large magnitude of the difference between the smallest and largest interaction strength weightings (~10,000-fold), the lines were weighted by the rank of the associated interaction strength, where the smallest interaction strength was given a rank of 1 and the largest a rank of 137 (the maximal number of realized interactions). The units are based on the inverse of the between-compartment density (0.0097).

In our scenarios for exploring compartments and stability, we made one simple assumption: the predators of the taxon involved in the disturbance compensated for the loss in their interactions by increasing their interaction strength with their remaining prey items. For the first hypothetical scenario, all interactions with taxon 36 were removed and the predators on 36 had their interaction strengths associated with 36 redistributed proportionally to their other prey interactions. For the second hypothetical scenario, all interactions associated with taxon 6 were removed except for those with taxa 5 and 8. The interactions of the predators on 6 were modified in the same manner as in the first scenario.

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Activation of the TRPC1 cation channel by metabotropic glutamate receptor mGluR1

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Group I metabotropic glutamate receptors (consisting of mGluR1 and mGluR5) are G-protein-coupled neurotransmitter receptors[1] that are found in the perisynaptic region of the post-synaptic membrane[2]. These receptors are not activated by single synaptic volleys but rather require bursts of activity[3–5]. They are implicated in many forms of neural plasticity including hippocampal long-term potentiation and depression[6–8], cerebellar long-term depression[8–11], associative learning[7,11], and cocaine addiction[12]. When activated, group I mGluRs engage two G-protein-dependent signalling mechanisms: stimulation of phospholipase C and activation of an unidentified, mixed-cation