images, demonstrating that the effect is not driven by incidental stimulus-related characteristics. Further, threatening — but not non-threatening — stimuli were judged as arriving earlier than scrambled versions of the same images, suggesting that the effect is driven specifically by responses to threatening stimuli.

Experiment 3 investigated whether reduced time-to-collision judgments could reflect a non-specific effect of seeing threatening stimuli, such as heightened arousal. Participants saw threatening or non-threatening stimuli for one second, immediately followed by a looming blue disc. If the effect we report is a non-specific effect of seeing threatening stimuli, time-to-collision judgments of the blue disc should be faster when preceded by images of threatening stimuli. Contrary to this prediction, priming images had no apparent effect on time-to-collision judgments of a semantically-neutral disc.

Threatening stimuli are perceived as approaching more rapidly than non-threatening stimuli, especially for those who are fearful of those objects. These results show, in contrast to the traditional view of looming as a purely optical cue to object approach [1], that perceiving the time of imminent collision is not entirely driven by purely optical cues, but is also subject to emotional modulation. Gibson and colleagues [1] pointed out that as an optical cue to imminent collision, visual looming is a direct perceptual indicator of threat. Our results suggest that the affective content of looming stimuli also affects perceived time-to-collision. Underestimating arrival time of threatening stimuli may thus serve an adaptive role in leading responses to err on the side of additional time for either fight or flight. Some perceptual biases appear only for explicit perceptual judgments, but not for visually-guided actions [5]. Thus, it is possible that the present effect reflects a purely perceptual distortion that might not affect actions, such as catching.

Recent findings have demonstrated that emotion modulates some basic aspects of perception, such as visual contrast sensitivity [6], but not others, such as auditory directional attention [7]. The selectivity of emotional effects on perception is consistent with anecdotal reports that specific phobias may induce category-specific distortions of perception [8]. Though we investigated variability in fear in an unselected sample (i.e. generally non-phobic), our results provide experimental evidence consistent with this proposal. Other recent results have also suggested that individual differences in fear, even in the non-clinical range, alter space perception. For example, fear of heights is associated with distorted perception of vertical distance [9], whereas claustrophobic fear is associated with increased size of the near space immediately surrounding the body [10]. The present results fit with and extend these by showing that emotion not only alters the perception of space as a static entity, but it also affects the perception of dynamically moving objects, such as those on a collision course with the observer.

Supplemental Information

Supplemental Information includes experimental procedures and two figures and can be found with this article online at http://dx.doi.org/10.1016/j.cub.2012.07.053.

References
1. Schiff, W., Caviness, J.A., and Gibson, J.J. (1962). Persistent fear responses in rhesus monkeys to the optical stimulus of "looming". Science 136, 982–983.
2. Ball, W., and Tronick, E. (1971). Infant responses to impending collision: Optical and real. Science 171, 818–820.
3. Regan, D., and Beverley, K.I. (1978). Looming detectors in the human visual pathway. Vis. Res. 18, 415–421.
4. Schiff, W., and Detwiler, M.L. (1979). Information used in judging impending collision. Perception 8, 647–658.
5. Witt, J.K., and Proffitt, D.R. (2007). Perceived slant: a dissociation between perception and action. Perception 36, 249–257.
6. Phelps, E.A., Ling, S., and Carrasco, M. (2006). Emotion facilitates perception and potentiates the perceptual benefits of attention. Psychol. Sci. 17, 292–299.
7. Borjon, J.I., Shepherd, S.V., Todorov, A., and Ghazanfar, A.A. (2011). Eye-gaze and arrow cues influence elementary sound perception. Proc. Bio. Sci. 278, 1997–2004.
8. Rachman, S., and Cuk, M. (1992). Fearful distortions. Behav. Res. Ther. 30, 583–589.
9. Teachman, B.A., Stefanucci, J.K., Clerkin, E.M., Cody, M.W., and Proffitt, D.R. (2008). A new mode of fear expression: Perceptual bias in height fear. Emotion 8, 296–301.
10. Lourenco, S.F., Longo, M.R., and Pathman, T. (2011). Near space and its relation to claustrophobic fear. Cognition 119, 448–453.

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Groups have a larger cognitive capacity than individuals

Takao Sasaki and Stephen C. Pratt

Increasing the number of options can paradoxically lead to worse decisions, a phenomenon known as cognitive overload [1]. This happens when an individual decision-maker attempts to digest information exceeding its processing capacity. Highly integrated groups, such as social insect colonies, make consensus decisions that combine the efforts of many members, suggesting that these groups can overcome individual limitations [2–4]. Here we report that an ant colony choosing a new nest site is less vulnerable to cognitive overload than an isolated ant making this decision on her own. We traced this improvement to differences in individual behavior. In whole colonies, each ant assesses only a small subset of available sites, and the colony combines their efforts to thoroughly explore all options. An isolated ant, on the other hand, must personally assess a larger number of sites to approach the same level of option coverage. By sharing the burden of assessment, the colony avoids overtaxing the abilities of its members.

Nest site selection by *Temnothorax* ants exemplifies collective decision-making without well-informed leaders [5]. When a colony must find a new home, it can choose the better of two new sites even when no single ant assesses both. Instead, comparison emerges from a competition between recruitment efforts. Upon finding a site, an ant recruits nestmates to it with a probability that depends on the site's quality, as determined by entrance diameter, cavity size, light level, and other features [6]. Her recruits make their own quality-dependent recruitment decisions, creating positive feedback that directs the colony towards the better nest. Consensus is further enhanced by a quorum rule that accelerates recruitment once a site's population has surpassed a threshold [5].

Although this process does not require individuals to compare sites, they have the ability to do so; an isolated ant that assesses two sites of different quality can reliably choose the better one [7]. We took advantage of this fact to compare the cognitive capacity of groups and individuals. We induced subjects (either whole colonies or isolated ants of *T. rugatulus*) to select a new nest in one of two conditions. In the simpler condition they chose between only two nests, one good and one poor. In the more challenging condition, they chose among eight options, four good and four poor (Figure 1A). Good nests differed only in having a smaller entrance, a strongly favored feature [6]. Decision performance was measured by noting which type of nest the subject moved into.

We found that individuals performed significantly worse when the number of options was eight rather than two, indicating that they experienced cognitive overload ($\chi^2 = 4.18$, N = 43, df = 1, p < 0.05). In the two-nest condition, over 80%

of ants chose a good nest, but in the eight-nest condition, only 50% did, indistinguishable from random performance. Colonies, on the other hand, performed equally well with either two or eight options, with at least 90% choosing a good nest in each condition ($\chi^2 = 0.36$, N = 40, df = 1, p = 0.55) (Figure 1B). Thus, colonies achieved a significantly higher decision performance in the face of increased processing load than did individuals (partial χ^2 test: $\chi^2 = 8.75$, N = 3, df = 3, p = 0.03).

We hypothesized that colonies better handle higher option numbers because their members do not have to assess as many sites as isolated individuals. If so, we predicted that each colony member visits a smaller number of nests than an isolated ant. To test this, we repeated the eight-nest treatment, but counted the number of sites visited by each ant. The results of this second experiment confirmed our prediction: isolated ants assessed significantly more sites than did colony members (Wilcoxon rank test: W = 1819, $N_{isolated} = 10$, $N_{colony} = 209$,

p < 0.01) (Figure 1C). Importantly, although each colony member visited very few sites, the colony collectively assessed all eight sites.

The inferior performance of isolated ants cannot be explained as a simple artifact of isolating these normally very social animals. Lone ants performed just as well as colonies when choosing between two sites; only with an increase in option number did their ability to select a good nest decline (Figure 1B). Nor can the colony advantage be ascribed to a higher probability of finding a good site. Because half of the options were good in both conditions, the probability of finding a good nest did not depend on the number of options available for either colonies or individuals (see the Supplemental Information for details). Furthermore, when isolated ants were tracked in the second experiment, all of them found at least one good nest. Indeed, they found many more sites than did all but a few individual colony members (Figure 1C). The small minority of colony members that visited a large number of nests contributed little to total transport effort, and thus to the colony's decision (see the Supplemental Information for details). Therefore, we attribute the worse performance of isolated ants to the difficulty of processing a greater load of data. We cannot say why isolated ants do not avoid this problem by simply assessing fewer sites. However, we speculate that they prolong their search for new nests because they lack social interactions, such as quorum attainment, that would normally trigger earlier acceptance of a site.

Cognitive overload is a growing issue for human decision-making, as unprecedented access to data poses new challenges to individual processing abilities [1]. Human groups also solve difficult problems better when each group member has only limited access to information [8]. For social insects, this advantage is likely much greater, because natural selection on colony-level phenotypes has shaped particularly elaborate and highly integrated group cognition. This is because selection acts largely through the reproductive success of whole colonies, rather than that of the sterile workers that make them up [9].
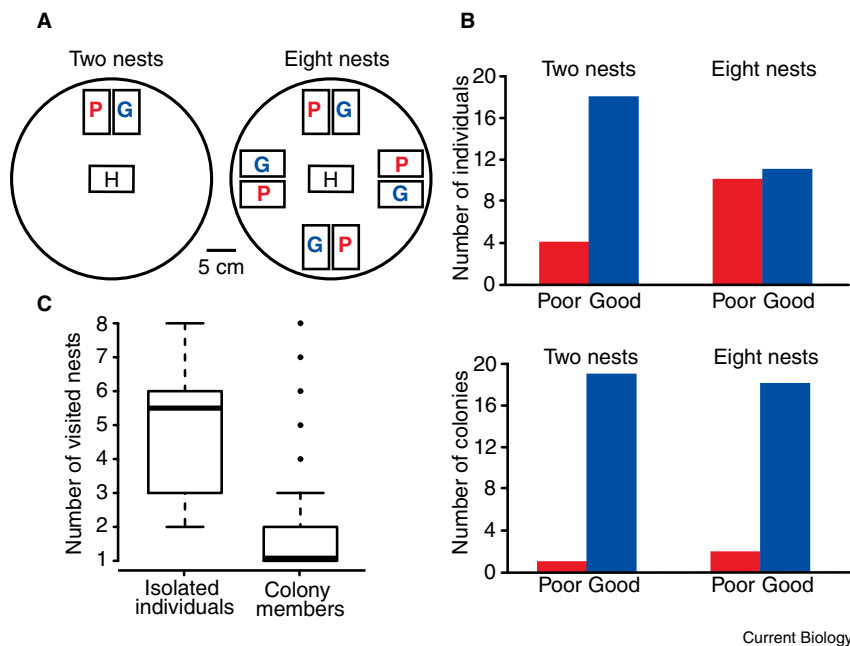

Figure 1. Effect of option number on decision performance.
(A) Experimental arenas. Subjects (whole colonies or isolated ants) were made to abandon their home nest (H) and choose a new nest from an array of either two or eight good (G) and poor (P) options. (B) Numbers of subjects choosing good or poor nests in each treatment. Isolated ants made worse decisions with eight options than with two (top chart), but colonies nearly always chose a good nest regardless of the number of options (bottom chart). (C) In the eight-nest condition, isolated ants visited more nests than did individual colony members. Boxes delimit the 1st and 3rd quartiles, the horizontal line indicates the median, and whiskers show the range. Open circles are outliers.

It has long been recognized that collective choice can improve accuracy by averaging out the random errors of inaccurate individual decisions [3]. The advantage we find here is different: rather than combining many essentially identical choices, colonies truly distribute their decision-making. No worker must carry out the full task of assessing and comparing all options, allowing the colony as a whole to process more information, more effectively. This advantage can serve as a model for the rapidly developing field of collective robotics, which looks to the robust, decentralized group behavior of social animals for biologically inspired design ideas [10].

References
1. Schwartz, B. (2004). The Paradox of Choice (New York: HarperCollins).
2. Thriner, G., Allen, C., and Goldstone, R. (2010). Recognizing group cognition. Cogn. Sys. Res. *11*, 378–395.
3. Couzin, I.D. (2009). Collective cognition in animal groups. Trends Cogn. Sci. *13*, 36–43.
4. Marshall, J.A.R., and Franks, N.R. (2009). Colony-level cognition. Curr. Biol. *19*, R395–R396.
5. Pratt, S.C., and Sumpter, D.J.T. (2006). A tunable algorithm for collective decision-making. Proc. Natl. Acad. Sci. USA *103*, 15906–15910.
6. Visscher, P.K. (2007). Group decision making in nest-site selection among social insects. Annu. Rev. Entomol. *52*, 255–275.
7. Sasaki, T., and Pratt, S.C. (2011). Emergence of group rationality from irrational individuals. Behav. Ecol. *22*, 276–281.
8. Kearns, M., and Suri, S. (2006). An experimental study of the coloring problem on human subject networks. Science *313*, 824–827.
9. Seeley, T.D. (1997). Honey bee colonies are group level adaptive units. The Am. Nat. *150*, S22–S41.
10. Zachery, R., Sastry, S.S., and Kumar, V. (2011). Special issue on swarming in natural and engineered systems. Proc. IEEE *99*, 1466–1469.

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Opponency of astringent and fat sensations

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In most cultures, people ingest a variety of astringent foods and beverages during meals, but the reasons for this practice are unclear. Many popular beliefs and heuristics, such as high tannin wines should be balanced with fatty foods, for example 'red wine with red meat', suggest that astringents such as pickles, sorbets, wines, and teas 'cleanse' the palate while eating. Oral astringents elicit 'dry, rough' sensations [1], in part, by breaking down mucinous lubricating proteins in saliva [2,3]. The introduction of oral lubricants, including fats, partially diminishes strong astringent sensations [4,5]. Thus, it appears that astringency and fattiness can oppose each other perceptually on an oral rheological spectrum. Most teas, wines, and 'palate cleansers', however, are only mildly astringent and an explanation of how they could oppose the fattiness of meals is lacking. Here, we demonstrate that weakly astringent stimuli can elicit strong sensations after repeated sampling. Astringency builds with exposures [6] to an asymptotic level determined by the structure and concentration of the compound. We also establish that multiple sips of a mild astringent solution, similar to a wine or tea, decrease oral fat sensations elicited by fatty food consumption when astringent and fatty stimuli alternate, mimicking the patterning that occurs during a real meal. Consequently, we reveal a principle underlying the international practice of 'palate cleansing'. Repeatedly alternating samples of astringent beverages with fatty foods yielded ratings of fattiness and astringency that were lower than if rinsing with water or if presented alone without alternation.

Three astringents — grape seed extract (GSE), epigallocatechin-gallate (EGCG) from green tea, and aluminum sulfate (Alum) — were evaluated by volunteers for perceived astringency intensity over the course of 80 oral exposures (sips). The astringency intensity curves grew exponentially over exposures, regardless of the compound or concentration (Figure 1A and Figure S1 in the Supplemental Information). Each astringent solution, however, elicited distinct maxima $(a + y0)$ depending on the concentration level. Weakly concentrated solutions never reached the astringency maxima of more concentrated solutions of the same compound. In addition, the rate (b) at which maximal intensity was reached over trials varied with both the chemical structure and concentration (Figure 1B). Here, Alum and EGCG solutions reach their astringency maxima faster at high concentrations than low, whereas GSE solutions reach their maximum at the same rate regardless of the concentration.

After establishing that weak astringents could elicit strong astringency with repeated sampling, we asked subjects to rate fattiness and astringency, after ingesting pieces of fatty food (dried meat) alternating with multiple sips of one of two rinsing solutions (tea or water). Astringent rinses affected oral sensations. In particular, the perceived fattiness was less pronounced after drinking tea than after drinking water (Figure 1C left panel). Thus, astringent consumption during meals provided a greater reduction of oral fattiness compared to water rinses. We also observed a more significant growth of astringency sensation with multiple sips without eating a fatty food, indicating that fat reduced the build-up of astringency (Figure 1C right panel). Similarly, there was a greater increase of fatty sensation from repeated fatty food consumption without any rinsing (Figure 1D left panel). These observations support the hypothesis that these sensations oppose each other perceptually and lie at different ends of an oral rheological/tribological sensory spectrum.

The oral perceptions of fattiness and astringency largely depend on tactile sensations [7]. Frictional rubbing of the oral epithelia is very important for food tactile perception. For example, foods are commonly assessed mechanically *ex vivo* using a tribometer, which measures the