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## Conflict Interference in an Insect

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Response conflicts occur when the correct goal-congruent response is weaker than an alternative but incorrect response. To overcome response conflicts, the stronger response has to be inhibited, making the study of response conflicts an important research topic in higher order cognition. Response conflicts often result in conflict interference—an increase in error rates and response times. Here, we ask whether an invertebrate—the ant, *Lasius niger*—can solve such response conflicts and, if so, whether it suffers from conflict interference. We also ask whether ants show congruency sequence effects, where subjects show transiently reduced conflict interference when conflicts repeat. We developed task-mimicking aspects of the Stroop color–word test, in which ants must learn to follow a neutral cue (a scent) on a Y maze but ignore a dominant and innately meaningful signal (a pheromone trail). The pheromone can be congruent with the scent cue (lead to the same maze arm) or be incongruent. Both accuracy and task-solving latency suffered when the information sources were incongruent. There was no evidence of congruency sequence effects. Because of limitations of the experimental design, we cannot rule out that insects would also show a congruency sequence effect under a different experimental paradigm. Although the methodology is not directly comparable to human studies, the presence of clear conflict interference suggests parallels between insect and human information processing, in spite of completely different brains. This powerful and straightforward methodology opens the possibility of exploring conflict interference in the presence of prepotent response tendencies in an invertebrate model. We hope this work encourages the field of response competition to use the vast literature on response competition in animal behavior studies.

**Keywords:** response conflict, conflict adaptation, Stroop test, prepotent response

**Supplemental materials:** <https://doi.org/10.1037/com0000294.supp>

Cognitive control in humans refers to the ability to carry out weaker but intended responses despite competition, with dominant, habitual responses for the sake of higher level goals (compare Dreisbach, 2012; Miller & Cohen, 2001). For example, while

crossing a street in a country with left-hand driving, you might experience a conflict between your strong habit of looking left before stepping onto the street and the actually appropriate action of checking the right side first. To deal with these so-called response conflicts, the human cognitive system is equipped with a monitoring entity that detects conflicts (i.e., the concurrent activation of conflicting response tendencies) in the ongoing processing stream. This information is used to adapt and improve performance in an immediately following conflict situation (Botvinick et al., 2001; Verguts & Notebaert, 2009).

Response conflict has been a topic of research in experimental psychology for a long time. Human conflict processing is typically investigated in response interference paradigms such as the Stroop word–color task (Littman et al., 2019; MacLeod, 1991; Stroop, 1935). In this task, participants are shown color names printed in various colors and have to name the color the word is printed in while ignoring the word itself. For literate people, reading the word is the more automatic response. Participants show higher response times (RTs) and higher error rates when the word meaning and its printed color are incongruent (e.g., red printed in blue) and faster RTs when word meaning and color are congruent (e.g., red printed in red; MacLeod, 1991). The reason for this effect is usually assumed to be that word reading is the faster, more automatic process than color naming and, therefore, has to be inhibited to avoid a prepotent and wrong response on incongruent trials. Conversely, on congruent trials, color naming profits from the congruent color word information (MacLeod, 1991).

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The order of congruent and incongruent trials in a trial sequence modulates the congruency effect: After an incongruent trial, performance on another incongruent trial is typically improved, whereas performance on congruent trials is hampered. This phenomenon is termed the congruency sequence effect or sequential conflict adaptation<sup>1</sup>. Sequential adaptation has been subject to a tremendous amount of research and theoretical debate in the past two decades (Botvinick, 2007; Botvinick et al., 2001; Dignath et al., 2019; Dreisbach & Fischer, 2015; Egner, 2007; Gratton et al., 1992; Verguts & Notebaert, 2009). Two broad types of accounts attempt to explain congruency sequence effects: one based on cognitive control and one based on associative learning.

The most prominent cognitive control account is the conflict monitoring theory by Botvinick et al. (2001). Their computational model describes how a response conflict, measured over the output layer of the model, is registered by a conflict monitor, which then sends signals to a task demand unit that in turn sends biasing signals to the input unit. These biasing signals make the input units transiently more sensitive to the goal-relevant information (in the case of a Stroop test, the color information) and less sensitive to the word information. As a consequence, an incongruent Stroop stimulus can be answered faster when it follows another incongruent Stroop stimulus (Botvinick et al., 2001). Even though the conflict monitoring theory has gained a lot of behavioral and also neurophysiological support (Kerns et al., 2004; Stürmer et al., 2002), its core assumptions have also been criticized: In many classical demonstrations of the congruency sequence effect, associative mechanisms cannot be ruled out, especially when only two stimulus features for target and distractor are used (Mayr et al., 2003). To illustrate this, take the example of a Stroop task with only red and blue as stimulus features. Four different stimulus configurations are possible: red as red, red as blue, blue as red, and blue as blue. Conflict monitoring theory predicts that congruent trials are faster when they follow another congruent trial than an incongruent trial and conversely that incongruent trials are slower following congruent trials than incongruent trials owing to increased cognitive control on trials following incongruent trials. However, incongruent trials following another incongruent trial are 50% identical stimulus repetitions. The same holds for congruent trials following congruent trials. Sequences from congruent to incongruent and vice versa never include such stimulus repetitions. In fact, when controlling for these direct stimulus repetitions, the usually observed congruency sequence effect disappears: Participants are slower on incongruent than on congruent trials, but this effect then is no longer modulated by the congruency in the preceding trials (Mayr et al., 2003)<sup>2</sup>. This was taken as evidence that conflict sequence effects can be explained in the absence of cognitive control by way of associative learning: The correct response on direct stimulus repetitions can be directly retrieved without assuming the contribution of a higher order task demand unit. The debate regarding the roles of associative learning versus cognitive control in the congruency sequence effect rages on (Braem et al., 2019; Egner, 2017).

The conflict monitoring account assumes the involvement of specific brain structures, namely, the dorsolateral prefrontal cortex and the anterior cingulate cortex (Botvinick, 2007). A neglected approach for testing this account is the comparative one, in which animals lacking these brain structures are tested for conflict interference and congruency sequence effects. Conveniently, response

conflict situations have been extensively studied in animals (de Haan, 1940; Swihart & Swihart, 1970; Szymanski, 1912). It has long been known that instinctive responses can interfere with learned responses in animals, for example, by adding unrewarded behaviors to a trained response, sometimes to the eventual exclusion of the trained response (Breland & Breland, 1961) or through the continued performance of an instinctive behavior even if it results in a cessation of reward (Williams & Williams, 1969). Haddon et al. (2008) developed an analogous paradigm to the Stroop interference task in rats and demonstrated interference by the overlearned response when rats were required to provide the undertrained response. Social insects such as bees (Cheng & Wignall, 2006; Chittka, 1998) and ants also experience response competition between learned responses. For example, Cheng and Wignall (2006) trained honeybees to locate a reward on one side of a colored landmark, and then trained the same bees to locate a reward on a differently colored target, with the landmark either staying the same, changing its color, or changing both its color and its location relative to the target. Strong interference was seen when a different response (visiting the opposite landmark side) was required, but not when the landmark color changed. The study of social versus private information conflict has been especially active (reviewed in Grüter & Leadbeater, 2014): In such experiments, focal animals must choose between responding to a social cue, for example, shoal-mate presence in fish (Kendal et al., 2005), pheromone trails in ants (Cronin, 2013), or alarm calls in birds (McLachlan et al., 2019), or to private information such as a neutral cue previously associated with food or shelter, or direct personal experience of danger. Previous conflict experiments already offered some information relevant to response interference in insects. Grüter et al. (2011) trained *Lasius niger* ants to find food on one arm of a T maze and then arranged for an innately attractive pheromone to be present on the opposite arm. They report a strong preference for following their memory over the pheromone trail, and no increase in response time. However, this study did not have an explicit correct and incorrect response, so it is not directly comparable with a conflict interference task.

Demonstrations of parallel neural and behavioral patterns in human and animal cognitive tests are already beginning to inform the debate on cognitive control: Czaczkes et al. (2018) demonstrate voluntary task switching in an ant in response to reward level changes, as previously shown in humans (Fröber & Dreisbach, 2016). de Wit et al. (2006) examined the neuronal basis of response conflict in rats—see Mansouri et al. (2009) for a review of the neuronal basis of conflict processing in humans and primates. Developing an insect model of conflict interference and behavioral adaptation may help inform the ongoing theoretical debate

<sup>1</sup> Some authors use this term interchangeably, whereas others differentiate between “sequential conflict adaptation” to emphasize the contribution of control processes and “conflict sequence effect” to describe the effect without implying the contribution of control processes (cf. Egner, 2017, p. 65)

<sup>2</sup> Note that Mayr et al. (2003) used the Erikson flanker task as conflict paradigm, where a central arrow gives the direction of the target response and is flanked by flanking arrows that can either point to the same or different response (e.g.,  $\lll$  vs.  $\>\lll$ ). Using this paradigm, they found the conflict sequence effect disappeared when stimulus repetitions were excluded.

about the impact of associative and cognitive processes in the congruency sequence effect.

Ants are adept associative learners (Oberhauser et al., 2019; Piqueret et al., 2019), readily learn cue contexts (De Agrò et al., 2020), and voluntarily switch between responding to different information sources (Czaczkes et al., 2019). If the associative accounts of the congruency sequence effects are correct, ants should also show such effects. However, given that ants lack an anterior cingulate cortex, they may not be expected to show congruency sequence effects according to neural conflict monitoring accounts. On the other hand, given ants' self-control abilities and ability to facultatively select from a range of information sources (Czaczkes et al., 2019; Wendt & Czaczkes, 2017), some sort of behavioral adaptation to response conflicts might be expected. Here, we developed a task that mimics the Stroop word-color task in ants. The dominant but irrelevant information source (comparable to the printed word meaning) is provided by a pheromone trail, which ants innately follow at a high rate (Hangartner, 1969; Koch & Czaczkes, 2020; von Thienen et al., 2014). The correct but not innately meaningful response (comparable to the printed color) is provided by a neutral odor cue. We create conflict through spatial incompatibility between the dominant and one weak response (cf. Lu & Proctor, 1995; Miles & Proctor, 2011).<sup>3</sup> The paradigm that we developed is closely related to, but not a direct analog of, the Stroop word-color task: In our task, the conflict is between an innate and learned response, rather than a learned and overlearned response. As such, it can also be seen as an analog of the antisaccade task (Coe & Munoz, 2017; Munoz & Everling, 2004). Using an instinctive response has the major benefit of not requiring extensive pretraining of every subject to the competing response. In this respect, it is in practical terms more like the traditional Stroop task than fully training-based animal analogs (Haddon et al., 2008), as the subjects (both ants and humans) enter the experiment with a strong response preference and have spent all their mature life making one particular response. However, it is important to note that although pheromone-following in ants can be subjected to learning (Wenig et al., 2021), it is an innate response, not an overlearned response as is word reading in the traditional Stroop task.

## Method

### Animal Maintenance

We used 11 queenless colony fragments of the black garden ant, *Lasius niger* (Linnaeus), collected from nine different colonies on the University of Regensburg campus. Colonies were housed in a plastic box (40 × 30 × 20 cm) with a layer of plaster on the bottom. Each box contained a circular plaster nest (14 cm diameter, 2 cm high). Colonies contained c. 1,000 workers and small amounts of brood. The ants were fed ad libitum on 1 M sucrose solution supplemented with *Drosophila melanogaster* fruit flies. Colonies were deprived of food for 4 days before each trial to give high and consistent motivation for foraging deposition. Water was provided ad libitum. A total of 69 individual ants were tested.

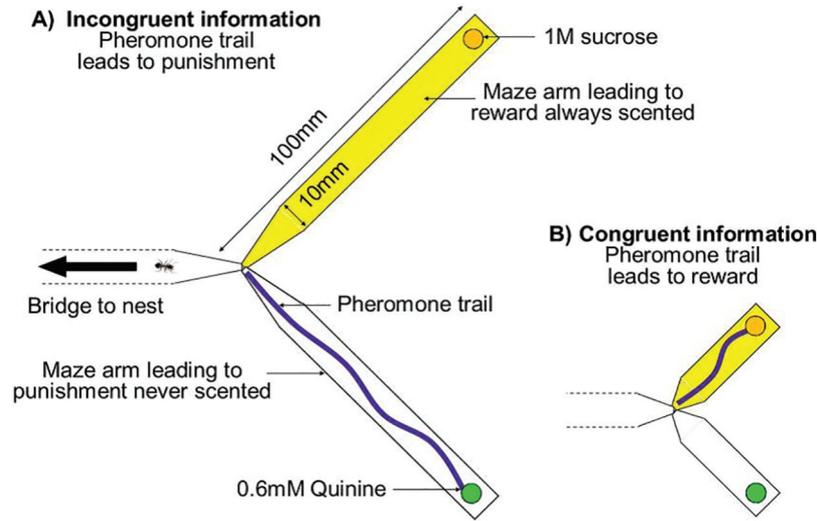
### Experimental Design

A Y maze (arms 10 cm long, 1 cm wide, tapering to points at the bifurcation) was created by assembling three replaceable paper overlays on raised platforms, following Czaczkes (2018). This was connected to a colony box via a drawbridge. A drop of reward (a 5-mm diameter drop of 1.5 M sucrose solution) or punishment (a drop of 60 mM quinine solution) was placed at the end of each arm (Figure 1). The paper overlays on the arm leading to the reward were always scented, by storing them in a sealed box containing a glass Petri dish with three 5-mm diameter drops of lemon essential oil on it for at least 24 hr. In addition, one of the overlays (either the scented one leading to the reward or the unscented one leading to punishment) was marked with a pheromone trail of realistic strength. A pheromone solution was produced by freeze-killing worker ants and dissecting out their hindguts under a stereomicroscope: The hindgut is the glandular source of the trail pheromone in *Lasius niger* (Bestmann et al., 1992). We then immersed eight worker hindgut glands in 2 ml of dichloromethane, following von Thienen et al. (2014), and stored the solution at −20 °C until needed. Throughout the experiment, to mark a runway arm with pheromone, 5.6 µl of this mixture was applied in an even line along the paper overlay covering the arm, using a capillary tube (10 µl calibrated pipettes, Servoprax GmbH, Wesel, Germany). This amount was calculated to produce a pheromone trail of a realistic strength (von Thienen et al., 2014) and elicits pheromone-following indistinguishable from a naturally laid trail (Czaczkes et al., 2019). Both the rewarded, lemon-scented side (target) and the pheromone-marked side (distractor) were varied pseudorandomly (Table 1). This rendered side and pheromone presence uninformative, whereas the lemon odor cue was maximally informative. As ants have a strong innate tendency to follow pheromone trails (Hangartner, 1969; Koch & Czaczkes, 2020; von Thienen et al., 2014), we expect pheromone trails to be strong *distractors* in this ant version of a conflict task, whereas following the odor cue is referred to as the *target* response. Trials in which the pheromone and odor cue both were located at the same arm of the Y maze are considered *congruent* trials, whereas a mismatch of the location of pheromone and odor was considered an *incongruent* trial.

### Experimental Procedure

A trial began by connecting the Y maze to a colony via a drawbridge. Several ants were allowed to freely walk up the bridge to the Y maze, where they encountered the pheromone trail and almost always followed it to the quinine solution, tasted the drop,

<sup>3</sup> Originally, we had planned a comparative study by developing a paradigm for humans where they have to learn by trial and error (without explicit instructions) how to respond correctly to arrows pointing either to the right or the left. The direction of the arrows was the irrelevant conflicting distractor information, and the color of the arrow, blue, or yellow, was the response relevant information that had to be learned. We found a conflict interference effect (worse performance when the arrow pointed into the response incongruent direction), but we only found a marginally significant conflict sequence effect in the first 24 trials (which turned highly significant in four additional blocks of 80 trials each). As these human data do not add any deep insights into the origin of sequence effects in humans, we decided not to present them here. Data and methods are available upon request.

**Figure 1***Setup of the Y Maze Used in the Ant Paradigm*

*Note.* The lemon-scented arm always leads to the reward, and the unscented arm leads to a punishment. A pheromone trail is also present, either leading to the punishment (A: incongruent configuration) or to the reward (B: congruent information). Figure 2A including the ant image shown, is shown to scale. See the online article for the color version of this figure.

and displayed aversive behavior (jerking back and grooming behavior). After some exploration, one ant discovered the sucrose solution at the end of the other arm and began drinking. She was then marked with a dot of acrylic paint on the abdomen, and all other ants were returned to the colony. The marked ant was allowed to drink to satiation, whereupon she freely returned to her nest to unload the sucrose solution. While in the nest, all overlays were replaced and rearranged according to the current treatment order being carried out (Table 1). The replacement of all overlays prevents any pheromone deposited by the experimental ant interfering with her own subsequent decisions. The marked ant was allowed to return to the Y maze, where it again eventually found the food source, drank, and returned. Ants were allowed to make up to 24 return visits in this manner, the first eight of which were considered training visits, but were structurally identical to the rest. A full run of 24 visits took on average just under 2 hr. On each visit, the initial arm choice of the ant (crossing a line 2 cm from the bifurcation) and the final arm choice (which droplet was first contacted) were noted. Trials were video recorded, and the time from entering the Y maze to making both the initial and final decision (initial and final decision latency) was extracted from the video.

## Statistical Analysis

The entire analysis code and output are provided in Supplement 1 in the online supplemental materials. We used general linear mixed-effect models (Bates et al., 2014, p. 4) implemented in R (R Core Team, 2018). In 95% of visits, the ants committed to the path they first chose. Corrections overwhelmingly occur when the ant initially made an error (12% of errors are corrected vs. 3% of

correct decisions are revised in error). As such, we focused our error rate analysis only on the final decision.

First, we asked whether current congruence state (congruent/incongruence) influenced final decision time and error rates. We included individual ant ID nested inside colony ID as random effects, to control for nonindependence of data. We then examined potential sequence effects on error rate and decision time by predicting these values according to sequence group, which is the current congruence state and the preceding congruence state. This results in four levels: congruent > congruent (cC); congruent > incongruent (cI); incongruent > congruent (iC); and incongruent > incongruent (iI).

Decision time was centered and scaled using the scale () function, which subtracts the mean from each value and then divides each value by the standard deviation, and modeled using a Gaussian distribution family. Error rates were analyzed using a binomial distribution and logit link function. Contrasts were examined using estimated marginal means (Lenth et al., 2020). For decision times, we excluded data from visits in which ants made an error, as errors by definition require more time to correct. However, a full analysis including nonexcluded ants is presented in Supplement 1 in the online supplemental materials and does not differ materially from the main analysis reported.

## Results

The full analysis code and output are provided in Supplement 1 in the online supplemental materials. The full raw data are provided in Supplement 2 in the online supplemental materials.

Error rates and decision time were significantly higher in incongruent trials compared with congruent trials (general linear mixed-effect model; error rates:  $Z = -5.0$ ,  $p < .0001$ ; decision times:  $T =$

**Table 1**  
Overview Over the 24-Trial Order Used

Trial	Odor	Pheromone	Congruency	Sequence
1	Left	Left	Congruent	N.A.
2	Right	Left	Incongruent	cI
3	Left	Right	Incongruent	iI
4	Right	Right	Congruent	iC
5	Right	Left	Incongruent	cI
6	Left	Left	Congruent	iC
7	Left	Right	Incongruent	cI
8	Right	Left	Incongruent	iI
9	Left	Right	Incongruent	iI
10	Right	Right	Congruent	iC
11	Left	Left	Congruent	cC
12	Right	Left	Incongruent	cI
13	Left	Right	Incongruent	iI
14	Left	Left	Congruent	iC
15	Right	Right	Congruent	cC
16	Left	Right	Incongruent	cI
17	Right	Left	Incongruent	iI
18	Left	Left	Congruent	iC
19	Right	Right	Congruent	cC
20	Right	Left	Incongruent	cI
21	Left	Right	Incongruent	iI
22	Left	Left	Congruent	iC
23	Right	Right	Congruent	cC
24	Right	Left	Incongruent	cI

*Note.* cC = congruent > congruent; cI = congruent > incongruent; iC = incongruent > congruent; and iI = incongruent > incongruent. Shaded region (first 8 visits) are considered as training visits, and not included in the statistical analysis, although they are structurally identical to the remaining 16 visits. The first eight trials were considered training to allow the ants to learn that pheromone trails are uninformative, whereas the lemon odor is fully informative. Two different layouts were used; this one and the exact mirrored layout so that the Congruency and Sequence columns apply for both layouts. This sequence was chosen to balance the rewarded side and prevent three repeats of a rewarded side, so as to avoid side learning and to avoid repeated alternations to avoid pattern learning. It was also designed to balance the number of times each sequence appeared and the sequence position in the trial order. Complete balancing was not possible, and hence there are fewer congruent trials (11) than incongruent ones (13).

–8.25,  $p < .0001$ ; see Figure 2A and 2C). However, there was no evidence for a sequence effect: Sequences with different current congruence states were different from each other ( $p$  for all contrasts  $\leq .002$ ), whereas sequences with similar current congruence states were not different ( $p$  for all contrasts  $\geq .18$ ; see Figure 2B and 2C, and online Supplement 1 in the online supplemental materials for complete statistical output).

## Discussion

Ants showed a strong conflict interference effect, with higher RTs and lower response accuracy during incongruent trials, even after extensive experience with the test situation. However, the ants did not show a congruency sequence effect, even though the paradigm we used was predestined for repetition benefits and thus associative learning (compare Hommel, 2004, and Mayr et al., 2003): Tasks in a paradigm with just four stimulus configurations, such as the one developed here, can be solved by relying on basic stimulus features.

Prima facia, our conflict interference results seem to be explainable by purely associative processes: If we assume that pheromone (P) acts merely as a conditional stimulus (CS), just like lemon

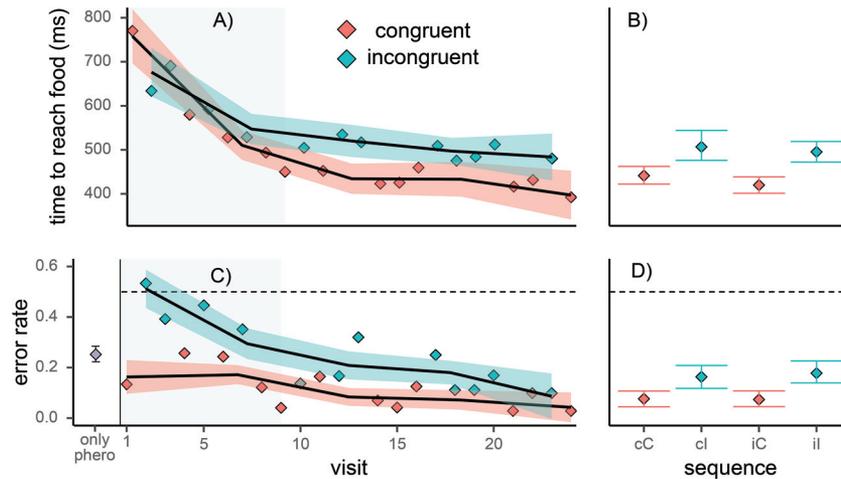
odor (L), then in congruent situations, both P and L are reinforced and no odor (N) is punished, although in conflict situations, L is reinforced, whereas P is punished. L is thus always rewarded, P is partially rewarded, and N is never rewarded. PL thus would have a much higher associative value than N, whereas L alone would only have a somewhat higher associative value than P alone. Discrimination between PL and N should thus be easier than between P and L. However, there are two reasons to reject a purely associative account. First, given that P already has innate positive value (it is innately attractive, as can be seen in the first congruent visit, Figure 2C, and in many previous studies [Koch & Czaczkas, 2020]), a purely associative account would predict a blocking effect when P is presented with L, such that the learning of the association between L and reward should actually be weakened. However, in the first incongruent trial, we see random choice, implying that the L association has perfectly balanced out the P effect. The preference for a cue rewarded once over no cue in *Lasius niger* ants is between 70% and 75% (Grüter et al., 2011; Oberhauser et al., 2019). Naïve ants follow pheromone trails on a bifurcation at a rate of circa 75% (Koch & Czaczkas, 2020). Thus, we would expect these two effects to balance each other out in the absence of blocking (as we observe), but not to do so if blocking was taking place. With blocking, we would expect preference for pheromone under 75% but above 50%. This lack of an observed blocking effect speaks against a purely associative account of our findings.

Second, in *Lasius niger*, trail pheromone is not subjected to negative associative learning: Wenig et al. (2021) demonstrate that although ants can learn to ignore pheromone information, they cannot learn to avoid it, even after extensive punishment with quinine or electric shocks. This again implies that responses to pheromone trails are not well-explained by a purely associative account. We thus maintain that our findings are best explained by conflict effects.

A potential explanation for the conflict effects is decision-making based on a drift-diffusion process (Bogacz, 2007; Brunton et al., 2013; Kacelnik et al., 2011; Ratcliff & McKoon, 2008)—specifically, a “tug-of-war” type process. In such a process, when choosing between options, the brain tracks the difference in the accumulating support for each option (thick black line, Figure 3). Thus, options with support from many information sources quickly accumulate enough support to surpass a decision threshold (Figure 3B). By contrast, with conflicting information, support for one option counters support for the others, slowing the decision-making process (Figure 3A). Indeed, as such processes are usually considered to have a stochastic element, conflicting information will also more often lead to making an erroneous decision. *Temnothorax* ants have been shown to use a drift-diffusion-like process when making individual decisions about nest-site preference (Sasaki et al., 2019).

Not finding a sequential adaptation effect in ants is interesting, but it does not rule out that such an effect may exist in insects. There are several major differences between our paradigm and those used to test for congruency sequence adaptation in humans. One difference, for example, is that our punishment (a highly distasteful quinine droplet) is likely a much stronger punishment than those inflicted on human subjects, which usually receive only error feedback. Another is that in the human task, subjects must suppress one task type (reading) in favor of another (labelling), whereas the ants are presumably staying in the same task type (identifying and following). Yet another is that humans often

**Figure 2**  
*Response Times and Error Rates*



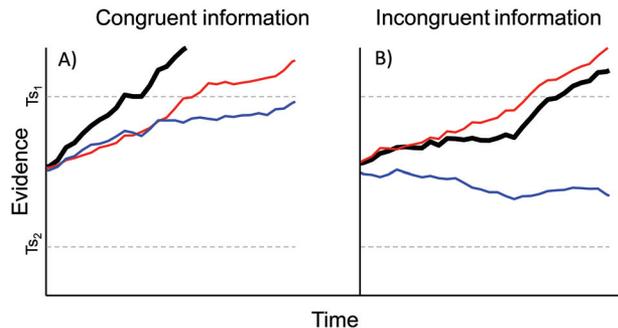
*Note.* (A) Time to reach food (milliseconds) over the course of the whole experiment (24 visits). The shaded area covers the first eight visits, which were a priori designated the training visits, and are excluded from our analyses. Red diamonds are congruent visit means, blue are incongruent visit means, black lines are smoothed conditional means, and ribbons are bootstrapped 95% confidence intervals for the means. (B) Mean Time to Reach Food by Sequence Group, With bootstrapped 95% Confidence Intervals. (C) as (A), but for error rates, dashed line is the null hypothesis of random choice. Lilac symbol labeled “only phero” represents the baseline pheromone following rate of naïve ants ( $n = 1,910$ ) on an identical setup, from Koch & Czaczkes (2020). (D) as (B), but for error rates. Note that the proportion of ants following pheromone on the first incongruent trial is 50% because of competition from the already-formed association between the odor cue and a reward during the first trial (which as part of the training phase was not included in the formal analysis, see Table 1). See the online article for the color version of this figure.

make hundreds of decisions in a single sitting, whereas our ants were limited to 16 test trials. It is possible that given a much larger sample size, sequence effects could be found, although given the nonetheless respectable sample size (300–525 data points per sequence) and lack of any hint of such effects, this seems unlikely. However, an important difference between this study and those conducted on humans is that the response actions in human task are much less complex in relation to the response action in the ant task. In the Y maze paradigm, the execution of one trial includes the choice of a certain path, actually walking the distance and either facing a potential reward or punishment at the end of the chosen path. Although human tasks also require the decision of which button to press and the execution of that button press, this clearly requires less effort and is thus less costly in case of an incorrect response. Finally, and to us the most important difference, the time between trials in a sequence is on the order of milliseconds in human tests but was on the order of minutes for ants. Such a delay may interfere with potential associative mechanisms. With that said, ants are well capable of forming associative memories in very similar paradigms (De Agrò et al., 2020; Oberhauser et al., 2019). Some researchers have particularly addressed the role of varying response–stimulus intervals (RSIs), that is, the time between one trial and the next, for the development of congruency sequence effects (Jiménez & Méndez, 2014). With extremely short RSIs (<200 ms) lower level effects are more likely than

adaptation of cognitive control. Rather long RSIs (>750 ms) might dilute accumulated effects of congruency, that is, larger interference effects after several congruent trials. In studies on dogs and ground squirrels, increasing delays between feedback has been shown to change choice patterns, favoring average over recent experiences (Devenport & Devenport, 1993, 1994). Ants may have experienced what we considered one single-step task as separate completed tasks of several single steps (choosing the path, walking the path, and drinking the drop; compare Monsell, 1996), which delayed feedback. One could conceivably develop a single step, <500 ms RSI task for ants, possibly involving harnessing individuals in a virtual-reality environment with automated feedback on microdecisions (as in the study by Brembs, 2008; Buatois et al., 2018; Goulard et al., 2020), and we encourage more tech-savvy researchers to take up this challenge. The benefit of the free-running paradigm we developed, compared with harnessing techniques, is greatly increased biological realism and much-reduced stress to the subjects. We also argue that intertrial intervals on the order of minutes are more ecologically valid than intertrial intervals of under half a second for both ants and humans. Perhaps focusing on more realistic intertrial intervals will highlight responses more likely to play a major role in real-world situations and deemphasize less important ones.

The clear conflict interference effects, even in free-running subjects and despite the large differences in methodology between our

**Figure 3**  
Two Drift-Diffusion Models



Note. Drift diffusion “tug-of-war model,” with stronger evidence (red/dark gray line) and weaker evidence (blue/light gray line). When both information sources agree (A, congruent information) the total support (thick black line) accumulates rapidly and quickly crosses the decision threshold (grey dashed lines,  $T_{s1}$  and  $T_{s2}$ ), resulting in a rapid decision. When information is incongruent (B), a “tug-of-war” ensues, and reaching a threshold takes longer, resulting in a longer delay. Another drift diffusion model in which the accumulators do not interact (the “horse-race” model, imagine no thick black line, first colored line to reach a threshold wins) would produce similar predictions for congruent situations, but predict much weaker effect sizes. See the online article for the color version of this figure.

study and ones on humans, demonstrates that this is a fruitful experimental direction to take. Future studies could take these ideas further by performing overlearning competition experiments, as a more direct analogy of the Stroop test. The preferential reliance on odor-associated cues rather than visually associated cues in these ants (Oberhauser et al., 2019) could be harnessed to emphasize such overlearning effects. Other model invertebrate systems with known and commercially available innately attractive pheromones, such as Argentine ants (*Linepithema humile*) or honey bees (*Apis mellifera*) could also easily be adapted for such conflict interference experiments.

This study is one in a long tradition of pitting innate or preferred responses against learned responses in animals (Andrade et al., 2001; de Haan, 1940; Kelber, 2002; Sun et al., 2020; Swihart & Swihart, 1970; Szymanski, 1912). We hope that by demonstrating clear differences and commonalities between human responses and those of an invertebrate model, this work encourages the field to also consider studies on invertebrates to gain new perspective and insights into anti-instinctive learning and conflict interference.

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