RAPID REPORT | *Higher Neural Functions and Behavior*

Action-based attention in *Drosophila melanogaster*

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[1]*Department of General Psychology, University of Padova, Padua, Italy;* [2]*Department of Biomedical Sciences, University of Padova, Padua, Italy;* [3]*Department of Biology, University of Padova, Padua, Italy;* and [4]*Padova Neuroscience Center, University of Padova, Padua, Italy*

Frighetto G, Zordan MA, Castiello U, Megighian A. Action-based attention in *Drosophila melanogaster*. *J Neurophysiol* 121: 2428–2432, 2019. First published May 1, 2019; doi:10.1152/jn.00164. 2019.—The mechanism of action selection is a widely shared fundamental process required by animals to interact with the environment and adapt to it. A key step in this process is the filtering of the "distracting" sensory inputs that may disturb action selection. Because it has been suggested that, in principle, action selection may also be processed by shared circuits in vertebrate and invertebrates, we wondered whether invertebrates show the ability to filter out "distracting" stimuli during a goal-directed action, as seen in vertebrates. In this experiment, action selection was studied in wild-type *Drosophila melanogaster* by investigating their reaction to the abrupt appearance of a visual distractor during an ongoing locomotor action directed to a visual target. We found that when the distractor was present, flies tended to shift the original trajectory toward it, thus acknowledging its presence, but they did not fully commit to it, suggesting that an inhibition process took place to continue the unfolding of the planned goal-directed action. To some extent flies appeared to take into account and represent motorically the distractor, but they did not engage in a complete change of their initial motor program in favor of the distractor. These results provide interesting insights into the selection-for-action mechanism, in a context requiring action-centered attention, that might have appeared rather early in the course of evolution.

NEW & NOTEWORTHY Action selection and maintenance of a goal-directed action require animals to ignore irrelevant "distracting" stimuli that might elicit alternative motor programs. In this study we observed, in *Drosophila melanogaster*, a top-down mechanism inhibiting the response toward salient stimuli, to accomplish a goal-directed action. These data highlight, for the first time in an invertebrate organism, that the action-based attention shown by higher organisms, such as humans and nonhuman primates, might have an ancestral origin.

goal-directed action; invertebrates; motor control; selection for action; walking

INTRODUCTION

Adaptive behavior utilizes neural information processing systems to allow interaction with the environment so as to maximize the probability of survival and reproduction. A key feature of this behavior in mammals is its selectivity. Relevant information has to be extracted by perceptual systems in a form that can be used to select the most appropriate action for the specific behavioral task (Cisek 2007). Selection mechanisms, on their side, have to block the many actions evoked by sensory inputs, except for the selected one. In the absence of these mechanisms, chaotic behavior is consequent (Riddoch et al. 2000).

In humans and primates, selection mechanisms are associated with selective attention (Castiello 1999; Tipper et al. 1998). The goal of selective attention is to provide sensory information that couples perception to action by selecting which object will be the target of the action and which action to use to reach the goal. However, under such conditions, information from nontarget objects "interferes" with the action directed toward the relevant target. The abrupt appearance of a distracting flanker nonobstacle object creates a perceptual representation of the "distracting" object, and attention is directed to it. This additional representation creates a conflict with that representing the original target object, resulting in a competition for access to higher processing levels and producing an alteration of the kinematics of the movement directed toward the original target (Castiello 1999).

Visual attention systems appear to operate by mapping out relevant perceptual aspects of the environment and translating them into an appropriate action also in invertebrates (Nityananda 2016). Similar mechanisms were observed in honeybees (Paulk et al. 2014) and in *Drosophila melanogaster* (Sareen et al. 2011) in studies where selective attention was deployed to optimize behavioral choices. On the other hand, to date, in invertebrates, there are no data regarding the role of "distracting" information in the form of the sudden appearance of a competing visual stimulus and whether it interferes with the engaged action toward a target.

Adapting a paradigm used in humans and primates (Sartori et al. 2014; Tipper et al. 1998), in the present study we tested whether flies engaged in a motor program to reach a target were affected by the appearance of a distractor stimulus in a way congruent with an action-centered attention theoretical framework. In our modified "Buridan paradigm," a distractor stripe (with respect to the fly's visual field) was presented while the fly was already moving toward another target stripe (Bülthoff et al. 1982; Neuser et al. 2008; Strauss and Heisenberg 1993). We hypothesized that the appearance of the distractor might determine three possible scenarios: *1*) if the presence of the distractor does not alter the originally pro-

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grammed direction of locomotion, then the fly's movement should proceed in the direction of the target, with no significant changes in the locomotion trajectory; *2*) if the presence of the distractor is inhibited in order for the fly to proceed in the originally planned direction, then some evidence of this inhibitory process might be detectable in the form of slight perturbations in the original locomotion trajectory; and *3*) if the presence of the distractor determines the initiation of an alternative motor program, which has the power to override the original one, then a dramatic change in direction toward the distractor should be evident.

We found that flies deployed an inhibitory mechanism operationalized in the form of trajectory changes without significantly interfering with the kinematics of the original target-bound action. These results raise interesting considerations regarding the nature of the selection-for-action mechanism in *D. melanogaster* and provide new data in support of an attention-like behavior. In particular, flies appear to inhibit the response toward a novel stimulus so as to complete an already activated motor program, in line with what has already been observed in humans and primates.

MATERIALS AND METHODS

Animals. The experiments were performed on 22 adult wild-type fruit flies (*D. melanogaster*, Oregon-R strain). All flies were reared on standard cornmeal-sucrose-yeast medium at 22°C in a 12:12-h light-dark cycle at 60% relative humidity. Fly crowding was controlled (20–30 flies each vial). Only individual 2- to 5-day-old male flies were used. For the experiment, flies were not previously starved. All experiments were conducted between zeitgeber times 2 and 4 at room temperature (22–23°C).

Experimental setup. To test how flies respond to the sudden appearance of a distractor stripe while freely walking toward a target stripe, we employed a cylindrical light-emitting-diode (LED) modular display (Reiser and Dickinson 2008) positioned around the fly, consisting of 48 (12 × 4) LED panels (each panel comprising an 8 × 8 LED array; IO Rodeo, Pasadena, CA). A custom-designed transparent arena (iMaterialise, Leuven, Belgium) was placed within the cylindrical LED display. The LED display and arena were mounted on solid stainless steel brackets fixed to an aluminum breadboard (Thorlabs, Newton, NJ), which was positioned on an anti-vibration table and covered with heavy black fabric draped over a wooden frame. The arena (maximum height at center = 3.5 mm; diameter = 109 mm) was designed so as to *1*) confine flies in two-dimensional (2-D) space, *2*) not allow the flies to reach the edge of the arena, and *3*) impede flight by means of a glass "ceiling" (Simon and Dickinson 2010). The arena was backlit by an infrared (IR) LED array (LIU850A; Thorlabs), and the IR light was diffused using paper diffusers. A charge-coupled device camera (Chameleon 3; FLIR System, Wilsonville, OR) with 1,288 × 964-pixel resolution, fitted with a 850-nm bandpass filter (MidOpt, Palatine, IL), was mounted 36 cm above the arena to record fly activity. Videos of flies moving in the arena were recorded at 21 frames/s. The experimenter could observe all events occurring within the arena through a high-definition webcam (C310; Logitech, Lausanne, Switzerland) mounted alongside the IR camera (Fig. 1*A*).

Software and management. The cylindrical LED display was controlled using MATLAB (The MathWorks, Natick, MA) scripts (Rei-
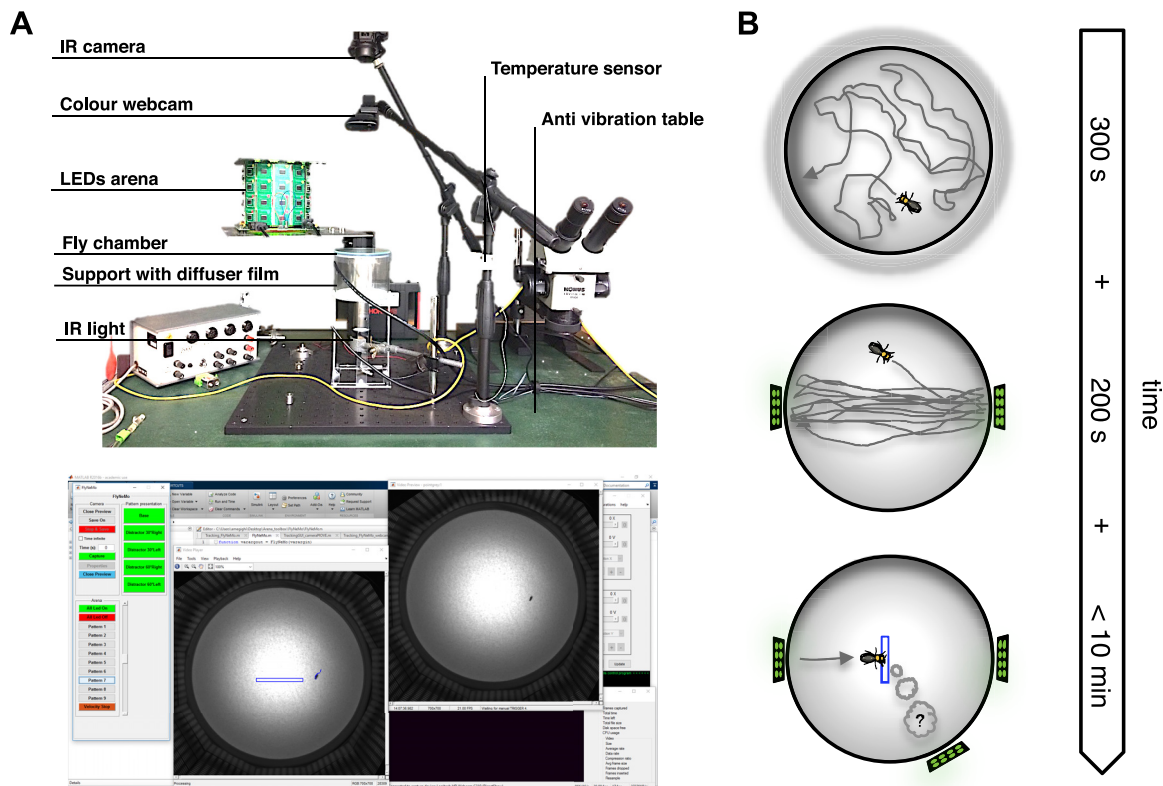

Fig. 1. Experimental setup and procedure. *A*: image showing the main components of the setup utilized (*top*) and a screenshot of the MATLAB custom graphical unit interface developed in our laboratory (*bottom*). *B*: cartoon showing the 3 phases involved in each experiment: acclimatization period in complete darkness for 300 s (*top*), 2 opposing bright green stripes switched on and behavior recorded for 200 s (*middle*), and behavioral task consisting in the random presentation of a distractor stripe at 60° whenever the fly crossed a virtual central window (blue rectangle; *bottom*). The behavioral task lasted a maximum of 10 min, after which the fly was removed regardless of the number of trials performed. IR, infrared; LEDs, light-emitting diodes.

Table 1. *Tracking analysis*

Condition	No. of Tracks	Velocity, mm/s	Distance, mm
No distractor	57	8.61 ± 5.56	43.05 ± 18.17
Distractor	33	8.22 ± 5.88	41.10 ± 19.17

Data are means ± SD.

ser and Dickinson 2008). The MATLAB Image Acquisition Toolbox was used for video recording. Furthermore, to identify when the fly's head entered the virtual central window within the circular arena, thus activating the visual patterns on the LED panels accordingly, we implemented a system for real-time tracking, adapting the FAST (features from accelerated segment test) method (Rosten and Drummond 2006) provided by the MATLAB Computer Vision System Toolbox. Online tracking analysis, video recording, and control of the LED arena were integrated into a single custom graphical unit interface, providing a unified software environment to manage all experimental variables. All the scheduled events involved in each experiment were automatically controlled by means of a custom script (Fig. 1*A*).

Procedure. Flies were individually loaded into the arena and were left to adapt in complete darkness for 5 min. Individual flies were then subjected to a Buridan paradigm, by illumination of two opposing bright stripes of 4 × 16 LEDs (width × height), each covering 15° width and 60° height of the fly's visual field when observed from the center of the arena. The classical interpretation of the phenomenon underlying this paradigm refers to the alternation between fixation and anti-fixation of attractive landmarks represented by contrasting stripes on a uniform background (Bülthoff et al. 1982; Horn and Wehner 1975; Maimon et al. 2008; Reiser and Dickinson 2008). In our experiments, individual fly locomotion, consisting in the fly continuously running to and fro between two opposing bright targets, was

initially recorded for 200 s. Flies that did not exhibit this behavior were not further considered (Kain et al. 2012). At this point the behavioral task proper was initiated. While the fly was still performing the Buridan paradigm, a third stripe (i.e., the "distractor") of the same dimensions as the other ones, was presented for 1 s when the fly crossed a virtual central window (27 mm × 3.6 mm) of the arena while running toward one of the original "targets" (Neuser et al. 2008). The distractor appeared to the right of the fly at an angle of 60°. The sequence of trials (i.e., distractor on or off) was randomly determined and counterbalanced across and within flies. Each fly performed the task for a maximum of 10 min, after which it was removed to avoid fatigue-determined bias (Fig. 1*B*).

Off-line tracking. To obtain an extensive definition of the fly's 2-D position and body orientation, we tracked the flies off-line using the CTRAX software (Branson et al. 2009).

Data preprocessing. The files obtained following the off-line tracking analysis were imported into R software (R Core Team 2017) for analysis with custom scripts. Only data from tracks in which single flies were directed toward the target were selected (i.e., all tracks in the opposite direction were removed). Table 1 summarizes these data.

Statistical approach. Repeated-measures analysis of variance was conducted using the *afex* R package (Singmann et al. 2018). Linear mixed models computed using the *lme4* R package (Bates et al. 2014) were employed to compare two shifting models, with or without the experimental manipulation as predictor. For model selection we used the Bayesian Information Criterion (BIC) (Schwarz 1978).

RESULTS

As a first step, we checked whether the path length (Fig. 2*A*) and the initial position of flies along the *y*-axis (Fig. 2*B*) and *x*-axis (Fig. 2*C*), as well as their orientation (Fig. 2*D*) and velocity (Fig. 2*E*), were uniformly distributed, to rule out any
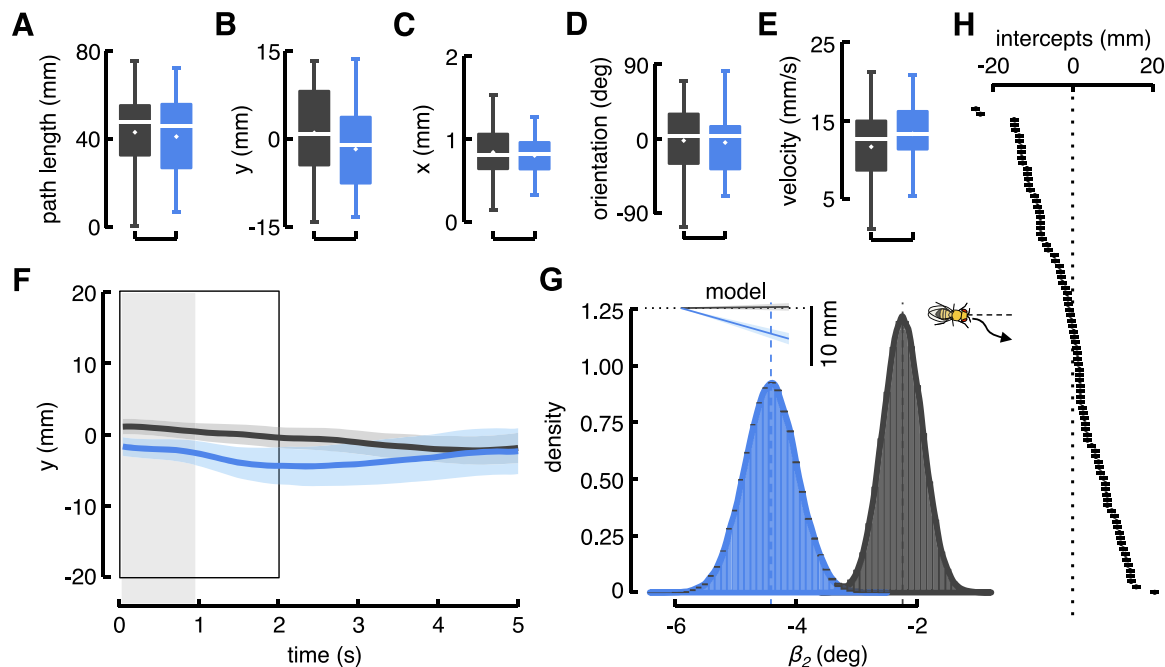

Fig. 2. Initial variables and distractor effect. *A*: boxplot of the path length in the no-distractor (black) and distractor (blue) conditions. *B*: boxplot of the flies' initial position along the *y*-axis. *C*: boxplot of the flies' initial position along the *x*-axis. *D*: boxplot of the flies' initial orientation. *E*: boxplot of the flies' initial forward velocity. *F*: plot of lateral shifting along the *y*-axis performed by flies, distinguished by condition. Data are average shifts (solid lines) per time; shaded lines represent SD. Shaded region represents the 1-s period of distractor appearance. The rectangular window represents the time interval used for modeling (i.e., 2 s). *G*: distribution of 100,000 bootstrapped model parameter values referring to the interaction between time and condition. *Top left inset* shows the shift modeled for condition, whereas *top right inset* shows a cartoon of the fly shifting consistently with distractor position. *H*: plot of random effect of the model. Dots represent each trial (known as best linear unbiased predictions), whereas horizontal lines crossing dots represent SE. Box defines first (Q1) and third (Q3) quartiles; bold horizontal white line is the median; white rhombus is the mean; whiskers define the lowest value still within 1.5 interquartile range [i.e., 1.5 × (Q3 − Q1)] of the lower quartile and the highest value still within the 1.5 interquartile range of the upper quartile.

influence by these variables on the subsequently measured trajectories. None of these variables showed significant differences between the two conditions [path length: $F_{(1, 88)} = 0.23$, $\eta^2 = 0.003$, $P = 0.63$; y-axis: $F_{(1, 88)} = 2.61$, $\eta^2 = 0.03$, $P = 0.11$; x-axis: $F_{(1, 88)} = 0.01$, $\eta^2 < 0.0001$, $P = 0.94$; orientation: $F_{(1, 88)} = 0.07$, $\eta^2 = 0.0008$, $P = 0.79$; velocity: $F_{(1, 88)} = 2.77$, $\eta^2 < 0.03$, $P = 0.10$]. This means that flies owned the same initial parameters regardless of the experimental condition.

Visual inspection of the average flies' position along the y-axis through time showed a slight lateral shift in the presence of the distractor with respect to its absence (Fig. 2F). For a more accurate understanding of this behavior, we focalized the analysis on the first 2 s of each trial, that is, during the distractor appearance and during the period 1 s after the distractor was turned off. We decided to extend this analysis beyond the period of distraction (i.e., 1 s) because the peak of lateral shift was evident at 2 s after the distractor onset. Because we were interested in the level of interference determined by the distractor, we linearly modeled the flies' position along the y-axis to understand how much flies changed their heading within this time window (rectangular window in Fig. 2F). We tested and compared two models, one with an interaction parameter between time and condition and the other with only time as a parameter (Table 2).

The model with the lower BIC value turned out to be the one with the interaction parameter (fixed effect, Fig. 2G, *top left inset*; random effect, Fig. 2H). The model shows that in the first 2 s of recording, the flies shifted slightly (4.42°) toward the distractor (Fig. 2G). Bootstrapping of the values related to the interaction parameter for each of the two conditions showed that the final distributions of the values shown by the distractor and no-distractor conditions did not overlap, implying a statistically significant difference between the two conditions ($P < 0.0001$). This basically means that, on a frame-by-frame basis, the flies showed a significantly greater lateral shift in the presence of the distractor than in its absence.

Overall, these results show that flies reacted to the distractor in a way that clearly indicates they acknowledged its presence, nonetheless maintaining their course toward the original target.

DISCUSSION

The primary aim of this study was to evaluate if, as observed in humans and primates, the abrupt presentation of a distracting flanker nonobstacle object to fruit flies would influence the already engaged locomotor action toward the original target. Our results indicate that the onset of the distractor seems to capture the attention of flies, initially inducing a significant shift in their trajectory in its direction compared with what occurs when no distractor was presented. This implies that flies acknowledged the presence of the distractor.

Table 2. *Model selection*

Model	df	BIC
$Y_{ij} = \beta_0 + \beta_2 X_{1i} \cdot D_{2i} + \lambda_i + \varepsilon_{ij}$	5	20,604.52
$Y_{ij} = \beta_0 + \beta_1 X_{1i} + \lambda_i + \varepsilon_{ij}$	4	20,604.70

Model parameters are shift along y-axis (Y_{ij}), time (X_1), condition (D_2), random effects (λ_i), and random error (ε_{ij}). df, degrees of freedom; BIC, Bayesian Information Criterion.

It has been already shown that invertebrates exhibit attention-like responses. In particular, freely moving insects display selective visual attention (Collett and Land 1975; Giurfa 2013; Nityananda 2016; van Swinderen 2011). Although it appears that attentional processes in invertebrates are elicited exogenously via bottom-up mechanisms, there is also evidence suggesting higher order modulation of attention via top-down mechanisms (Nityananda 2016).

Our data confirmed that the abrupt onset of a flanker "distractor" evoked a bottom-up attentional response in flies. Indeed, the observed reaction following the presentation of a distractor suggests that the sudden appearance of a distractor in the fly's visual field evoked changes in the motor responses. Recently, by employing a Buridan paradigm version comparable to ours in freely walking flies, it was shown how the presence of distractors evokes the flies' distractibility (Kirszenblat et al. 2018). However, our experiment did not address selective visual attention by exploring it from the point of view of the sensory input, but rather whether, once a visual target has been selected for an action implementation, the motor program may be affected by the processing of a distracting visual input. This question is embedded in the selection-for-action theory, according to which to minimize the action-interference effects, the information has to be inhibited from the motor perspective (Allport 1987).

Consistent with this theory, our data showed that flies changed their trajectories only partially toward the distractor, as evident in the trajectory angle of 4.42° compared with the distractor angulation of 60°. Flies remained much closer to the target during the distraction, and then, once the distractor disappeared, they finalized the original target-oriented motor program. This process would correspond to the formation of an additional motor representation for the "new object," conflicting with that already active for the target object. At this point it is reasonable to surmise that a top-down mechanism would be required to solve the conflict and select the right action. Namely, flies deployed an inhibitory mechanism operationalized in the form of trajectory changes to maintain the original target-bound action.

As previously found for humans and primates, the sudden appearance of a distractor object reaches a level of relevance similar to that of the target, activating a competition between the actions evoked by the target and the distractor. In other words, each object generates a parallel kinematic plan for action, determining an interference between "the intended but not-executed" action toward the distractor and the "intended and executed" action toward the target. The level of interference is proportional to the visual salience of the distractor (Castiello 1996, 1999). Specifically, a perceptuomotor representation for the new object, which conflicts with that already active for the target, generates a competition for higher levels of processing. This results in an alteration of the kinematics of the engaged action toward the target (Castiello 1999).

Notwithstanding our interpretation, one particular concern is that this behavior could simply be due to phototaxis (McEwen 1918). However, *1*) the distractor is of exactly the same size and luminosity as the original target (i.e., it is a visual object that elicits fixation, as is the case for the original target; see MATERIALS AND METHODS), and *2*) the ensuing motion of the flies is still directed toward the original target (i.e., it is not the case that the new trajectory is directed toward a point situated

midway between the target and the distractor, as expected in the case of phototactic response; Fraenkel and Gunn 1961), which suggests that the observed response of the flies was rather a consequence of their attention being temporarily captured by the flanker before being inhibited.

Given the importance of action-selection mechanisms in animal behavior, we believe that the novel evidence presented in this report for such phenomena in a highly tractable model organism such as *D. melanogaster* provides an important basis for a more detailed exploration of the relationship between environmental stimuli and motor responses, as well as of the neural circuitry involved in the visuomotor integration underlying such processes.

It is currently unclear whether flies and humans independently evolved selection-for-action mechanisms or whether they share the same mechanisms through a common ancestral neural circuit subserving this process. It has however been suggested that the vertebrate basal ganglia and the arthropod central complex share an evolutionarily conserved developmental genetic program and that these two neural structures may also share an involvement in the selection and maintenance of actions (Strausfeld and Hirth 2013). This an interesting avenue that further research should pursue.

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GRANTS

DISCLOSURES

No conflicts of interest, financial or otherwise, are declared by the authors.

AUTHOR CONTRIBUTIONS

G.F., M.A.Z., U.C., and A.M. conceived and designed research; G.F. performed experiments; G.F. analyzed data; G.F., M.A.Z., U.C., and A.M. interpreted results of experiments; G.F. prepared figures; G.F. drafted manuscript; G.F., M.A.Z., U.C., and A.M. edited and revised manuscript; G.F., M.A.Z., U.C., and A.M. approved final version of manuscript.

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