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The Kanizsa triangle illusion in foraging ants

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ABSTRACT

The Kanizsa triangle, wherein three Pac-Man configurations symmetrically face inwards, is a well-known illusion. By exposing foraging ants (*Lasius niger*) to Kanizsa-shaped honeydew solutions, we studied the origin of this illusion. More specifically, we examined whether foraging ants showed different movement reactions to local honeydew patterns formed by nestmates. This novel phenomenon could serve as an abstract model of the Kanizsa triangle illusion under the assumption that such an illusion could arise through the sum of each agent's limited global cognitions, because each agent could not perceive the entire subjective contours. Even a subjective consciousness consists of some parts which have no identical perception and could be an illusion. We succeeded in inducing foragers to move along the sides of a Kanizsa triangle when Pac-Man-shaped inducers were introduced. Furthermore, foragers appeared to form Y-shaped trajectories when dot-shaped or inverse Kanizsa inducers were used. Based on our findings, we propose an agent-based ant model that compares modelled behaviour with experimental phenomena. Our abstract model could be used to explain such cognitive phenomena for bottom-up processes, because ants cannot perceive the given subjective contours, instead simply move along the edges.

1. Introduction

The Kanizsa triangle, wherein three Pac-Man configurations symmetrically face inwards, is a well-known illusion (Kanizsa, 1976, 1979) that induces the perception of subjective, illusory contours. Illusory contours have been widely investigated in non-human animals (Bravo et al., 1988; Nieder, 2002; Sáry et al., 2008; Sovrano and Bisazza, 2009). Numerous research studies have focused on whether animals, including humans, perceive the illusion as entire pictures or in parts as its individual elements (Fujita, 2001; Hopkins and Washburn, 2002; Nagasaka et al., 2005; Vallortigara et al., 2008). Nevertheless, there appears to be a tendency within animals and humans to judge whether the part or the entire illusion is true or not, assuming that each level is independent of the other. Some studies have reported that the persistency of experimental subjects to either a part or the entire illusion changes depending on situational contexts (Matsukawa et al., 2004).

Several studies report that the Kanizsa illusion can be derived from differentiation–integration approaches (Gillam and Nakayama, 2002; Kogo et al., 2010). In these studies, local information detected by differentiations appears to create contours through integration (Gillam and Nakayama, 2002; Kogo et al., 2010). Tani et al. (2014) demonstrated that the plasmodium of *Physarum* displayed a Kanizsa triangle illusion because it integrated two levels of computation, i.e. lower and higher. In their model, local detection of environmental stimulus and asynchronous transportation of protoplasm appeared to enable agents to synthesise the differentiation–integration process (Tani et al., 2014). In these studies, wide-area space cognitions of agents are based on limited-area space geometries.

In this study, we demonstrated whether the Kanizsa triangle illusion arouse by foraging ants. Individual ants and the plasmodium of *Physarum* appear to sometimes use limited local information to estimate unknown food locations (Detrain and Deneubourg, 2006). Thus, each forager might use local information to detect surrounding spaces. Recently, we investigated whether the Muller–Lyer illusion could be perceived by foraging ants, where shaft lengths appeared to vary depending on arrow angles (Sakiyama and Gunji, 2013). In that study, foraging ants were exposed to arrow-shaped honeydew food, and their positions were tracked. Furthermore, we developed an abstract simulation model in which each agent (ant) affected the probability of stopping using surrounding agents. Therefore, each ant was regarded as an individual retinal cell.

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Ants cannot directly use global information but appear to flexibly use local information (Deneubourg et al., 1983; Mailleux et al., 2000; Jeanson et al., 2004; Detrain and Deneubourg, 2006; Wehner et al., 2006; Zeil, 2012; Cheng, 2012). Decision making on an individual level may play a role in realising global—i.e. colony level—profits (Detrain and Deneubourg, 2006). In our previous model, each agent anticipated undiscovered food locations based on the local perceptions of other agents by affecting the probability of stopping. Therefore, ambiguous global properties can be established by accumulating local information.

In our present study, we compare tracking the trajectories of foragers by exposing them to Kanizsa-shaped food with an abstract model in which entire subjective contours are produced based on bottom-up processes, i.e. by summing the reactions of each agent (or the trajectories of each agent) to local information. Here, by exposing a *Lasius niger* ant colony to a Kanizsa triangle composed of honeydew solutions, we study the origin of this illusion by excluding transcendence perspectives. In the current study, the global properties of the agents are their trajectories. Global space ambiguities for agents, such as where they should go, must be accumulated by local conditions (e.g. local honeydew patterns formed by nestmates).

Note that the concept of global space cognitions for each ant does not imply an entirety of perceptions or the ability to perceive the perfect subjective contours. Therefore, we do not demonstrate that each ant perceives the full subjective contours using local cues. Rather, we demonstrate that the full subjective contours might be constructed by summing the global space cognitions of each agent. If each ant in a colony can correspond to a neuron or retinal cell, then the behaviour of a swarm of ants can correspond to the behaviour of a neurological field. In this context, each ant might not see an illusion but rather that a swarm of ants might see the illusion.

Even a subjective consciousness consists of some parts which have no identical perception and could be an illusion (Wegner, 2002), which can be compared to a swarm of ants without common perception. Subjective contours can arise from stacking the trajectories of each ant, in particular, the directions in which they move after consuming the honeydew solution. It may give us a new knowledge on the implementation of the global property embedded in local interaction in a human visual system.

When ants were exposed to the Kanizsa triangle-shaped figures, we observed triangular trajectories along the mouth of each Pac-Man configuration. In addition, we developed an agent-based ant model in which each agent anticipated food based on the existence of other local agents. In such situations, the agent stopped with a certain probability. Otherwise, the agent went straight to avoid other agents. Thus, based on local circumstances, agents hold the balance between exploitation and exploration (Detrain and Deneubourg, 2006). Later, we show that these mechanisms could explain the phenomenological results of ant experiments.

2. Materials and methods

2.1. Rearing conditions

We studied three *Lasius niger* queen-less colonies with 400–600 workers. One colony was collected at Kobe University, and two test conditions were investigated using this colony. The remaining two colonies were collected at Waseda University, and one test condition was investigated using these colonies. All colonies were housed in plastic foraging boxes with dimensions of 35.1 cm × 25.5 cm × 6.1 cm (height). Each foraging box contained a plastic nestbox with dimensions of 5.1 cm × 5.5 cm × 1.1 cm (height), which were covered with clear-red plastic sheets. The walls of each foraging box were coated with talcum powder to prevent the ants from escaping. All experiments were conducted in a room with artificial light and the temperature was maintained at ±26.1 °C. We fed the colonies twice a week with honeydew and once a week with mealworms and freshwater was constantly available. Before our experiments, each colony was starved for 4–5 days to ensure that the ants would swarm.

2.2. Experimental setup

We brush-painted honeydew solution (50% w/w) on cardboard in the shape of the Kanizsa triangle using templates cut from a transparent plastic sheet. The resulting figure (Fig. 1A) consisted of three Pac-Man configurations symmetrically positioned, each with a diameter of 1.4 cm. The distance between the centres of two adjacent Pac-Man configurations was 4.0 cm. Therefore, the sides of the each triangle illusion were 4.0 cm. We set control experiments using figures consisting of three simple dots (Fig. 1B) and an inverse Kanizsa figure (Fig. 1C). Each dot or Pac-Man configuration in the control set was similarly 1.4 cm in diameter and positioned the same way as with the Kanizsa triangle. The inverse Kanizsa figure consisted of three Pac-Man configurations as inducers; however, each Pac-Man configuration was positioned with its 'mouth' facing outwards, as shown in Fig. 1C.

The cardboard on which these figures were painted was installed in a plastic foraging box. The swarm patterns of agents were recorded with a video camera (SONY). For each figure (i.e. the Kanizsa triangle, three dots and inverse Kanizsa triangle), only one trial was conducted on each experimental day. Each trial lasted approximately 10–20 min. We halted each trial when the honeydew solution was entirely consumed by the foragers. For the colony collected at Kobe University, the trial sequences (i.e. Kanizsa then the control set or control set then Kanizsa) were conducted evenly. The two colonies collected at Waseda University were used only for the inverse Kanizsa triangle, and each colony was tested once a day. Four trials were conducted for each of these figures.

To track the trajectories of foragers and obtain x–y coordinates at five frames per second, we used image-processing software

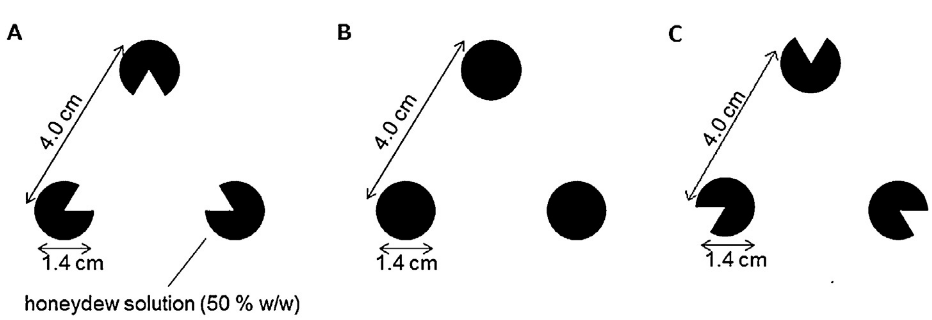

Fig. 1. Schematic examples of experimental stimulus. (A) Kanizsa triangle illusion figure. (B) Figure for the three dots experiments. (C) Figures for the inverse Kanizsa experiments.