



Short Communication

Evolution of social attentional cues: Evidence from the archerfish

Keren Leadner^{a,b,*}, Liora Sekely^{a,b}, Raymond M. Klein^c, Shai Gabay^{a,b,*}^a Department of Psychology, University of Haifa, Haifa 3498838, Israel^b The Institute of Information Processing and Decision Making, University of Haifa, Haifa 3498838, Israel^c Department of Psychology and Neuroscience, Dalhousie University, Halifax, Nova Scotia B3H 4R2, Canada

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ABSTRACT

Social cues such as gaze, head, and body orientation are essential for the survival of any social animal. The gaze cuing paradigm is a well-studied experimental manipulation, employed to detect automatic attentional shifts in humans. To the best of our knowledge, no previous study has tested non-primates in a paradigm that is similar to the one typically used on humans. Herein, three archerfish observed a conspecific picture oriented toward the right or the left, followed unpredictably by a visual target presented in the socially cued or un-cued location. Similar to the pattern observed in humans, fish demonstrated faster reaction times for targets presented at the socially cued location. Results suggest that social cues may have an early evolutionary origin and can elicit automatic attentional orienting even in species without a visual cortex.

1. Introduction

Many different animals live in social groups. Living in a group can have positive and negative outcomes for the individual. One example of a negative outcome that arises when living in proximity to conspecifics can be found in the electric fish *Gymnarchus niloticus* (Heiligenberg, W., 1975). This species uses electric signals to electrolocate objects in the surroundings. Yet, the electric signals of other nearby fish that employ a similar frequency can interfere with the fish's ability to use its own electric organ. Hence the fish adjusts its frequency so it will not be jammed by the conspecific's electric signals. This is a fascinating demonstration of a sensory system adjustment to the presence of a nearby conspecific. One example of a positive outcome of living in a social group is demonstrated by the archerfish that can learn complex sensorimotor skills just by observing the actions of members of their group (Schuster, Wöhl, Griebisch, & Klostermeier, 2006).

The ability to learn from observing using a conspecific's behavior (e.g., body or gaze orientation) as a social cue is highly adaptive. Social cues have many evolutionary advantages such as signaling an approaching predator and giving the group a warning signal to seek a hiding place (Friesen & Kingstone, 1998). Many animals make use of signals they observe in both conspecifics and members of other species (Emery, 2000; Frith & Frith, 2007). Social attentional effects have been observed in chimpanzees (Tomasello, Hare, & Agnetta, 1999), dogs (Hare & Tomasello, 1999), and even goats (Kaminski, Riedel, Call, &

Tomasello, 2005). Wild jackdaws (Davidson, Clayton, & Thornton, 2015) and crows (Clucas, Marzluff, Mackovjak, & Palmquist, 2013) detect and interpret human gaze as a potential threat. It was even demonstrated that pack living dogs and wolves followed their pack members' gaze in spontaneous interactions (Werhahn, Sommesse, & Range, 2016).

Humans and other primates are known to shift attention automatically according to human gaze direction (Frith & Frith, 2007; Shepherd, 2010). The gaze cuing paradigm was developed to detect attentional shifts, elicited by a social cue (Friesen, Moore, & Kingstone, 2005). In a typical version of this task, participants are shown a face-like stimulus looking laterally. Participants respond faster to targets presented in the socially cued location compared to the uncued location, even when the social cues are not informative about the upcoming target location. From these findings, it was concluded that a reflexive attentional process is involved in gaze cuing (Driver et al., 1999; Friesen et al., 2005; Friesen & Kingstone, 1998; Langton & Bruce, 1999). This phenomenon was also observed in primates (Deaner & Platt, 2003) and has been suggested to involve circuits in the temporal and parietal cortex (Hoffman & Haxby, 2000). Reflexive attentional orienting following gaze direction has been considered specific to higher primates (Ghazanfar & Santos, 2004). It has yet to be determined if reflexive attentional shifts, elicited by others' social cues, exists only in higher primates or if it is a general trait shared by other lower order animals (e.g., fish).

The relevant information that can be used as social cues differs

* Corresponding authors at: Department of Psychology, University of Haifa, Haifa 3498838, Israel.

E-mail addresses: kerenleadner@gmail.com (K. Leadner), sgabay@psy.haifa.ac.il (S. Gabay).

between different species. Some non-primate animals have undeveloped to non-existent facial musculature and have to move their entire head to direct their gaze (Emery, 2000). For those species (e.g., fish) head orientation might be the most relevant source of social information. Fish as a taxonomic group diverged from other vertebrates ~450 million years ago (Kumar & Hedges, 1998) and therefore can provide indications about structures and behaviors conserved across the animal kingdom (Karoubi, Segev, & Wullimann, 2016).

In the wild, the archerfish rapidly and accurately spits water jets at insects above water level (Karoubi et al., 2016). This ability can be employed for controlled behavioral experiments in which the fish is trained to shoot at artificial targets presented on a computer monitor (Gabay, Leibovich, Ben-Simon, Henik, & Segev, 2013) similar to

experiments studying human cognition (see Fig. 1). Archerfish are particularly ideal for studying the influence of social cues, as when they are first learning to shoot, they hunt in small schools, such that young archerfish are required to interact socially with their peers.

2. Methods

The experiment was conducted in accordance with Haifa University regulations and the State of Israel’s laws on animal care and experimentation. Our experiment involved testing three archerfish that were trained separately, similarly to previous studies on archerfish attention (Gabay et al., 2013).

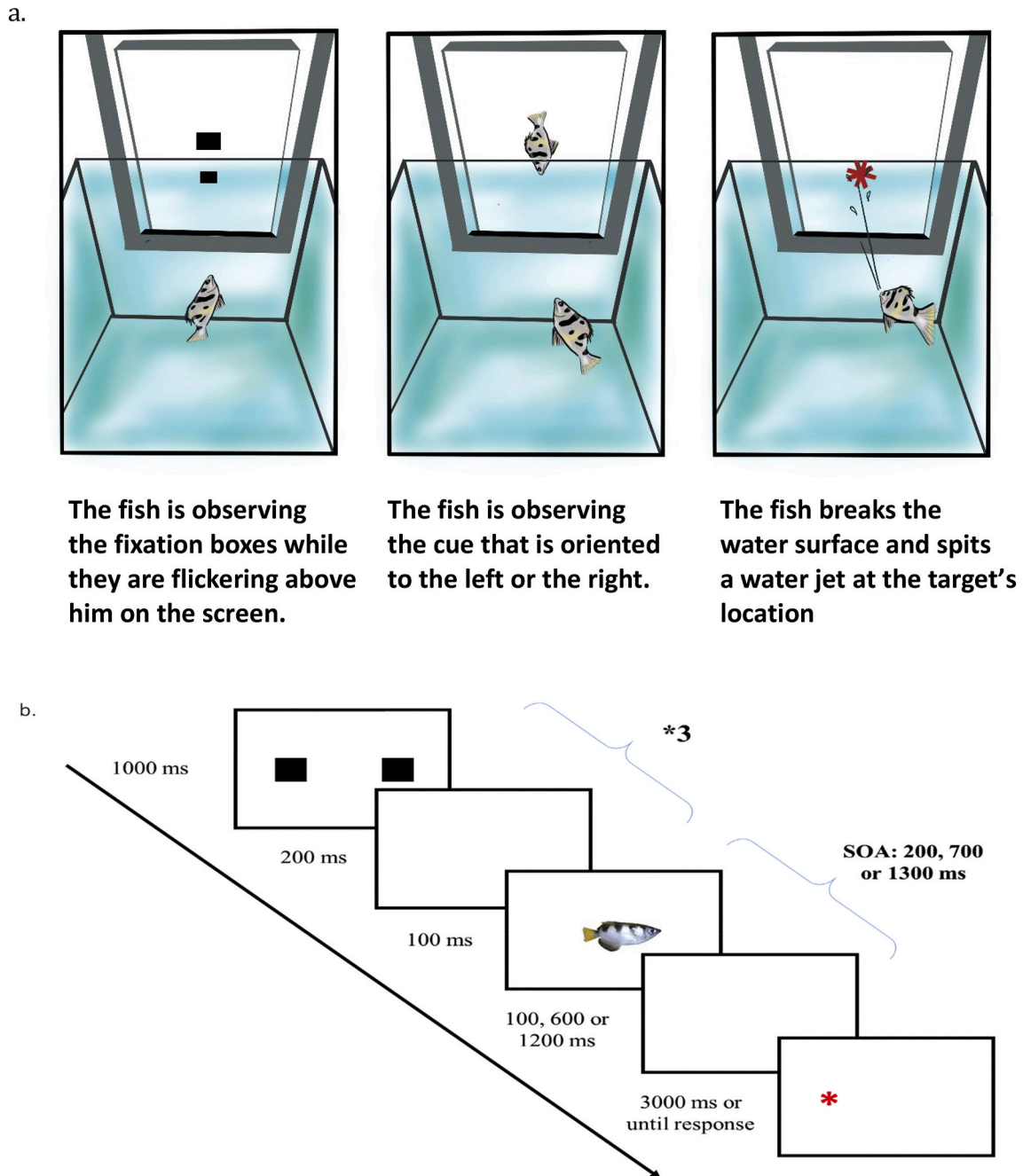


Fig. 1. The experimental procedure.

(a) The experimental setup and a fish performing the task (for a picture of the experimental setup see supplementary material) (b) The typical sequence of events in an invalid trial.

2.1. Apparatus

Each fish swam freely in a specially arranged water tank during and between experimental sessions. A 21-in. Samsung LCD monitor (model S24C650PL) was placed on a glass shelf 41 cm above water level. The fish were trained to shoot water jets at the target (a red asterisk). Sessions were recorded using a pair of GigE color (120 fps 640 × 480 1/4) cameras. One camera recorded the screen, and the other camera recorded the fish. The videos were analyzed using the Observer XT software for behavioral coding (Noldus). The software Synchronizes recorded videos and markers received for each event in the trial from E-prime 2 (Psychology Software Tools., Pittsburgh, PA) in which the experiment was built and presented. Reaction time (RT) was calculated by measuring the time from target appearance until the fish broke the water surface and started shooting (shooting onset). This was done by shifting the video timeline to the target marker and finding the frame in which the fish started its spitting behavior (the first frame in which the water jet originating from the fish mouth was detected). After marking the response initiation frame, the video timeline was shifted to the following target marker, skipping the cue presentation section. Using this procedure, the person marking the fish spit was unaware of the specific trial condition of each response. After marking the fish responses, reaction time for each trial was calculated by subtracting the time point in which the target was presented from the time point in which response was initiated. Successful shots were determined when the water jet landed on the surface of the target (see Fig. 1a). After each successful shot, the

fish received a pellet of food, and the experimenter cleaned the water from the glass shelf.

2.1.1. Procedure

Each trial began with the flickering of two black fixation boxes three times. For each cycle, the two boxes were shown for 200 ms, followed by a blank screen for 600 ms. After the last blank screen, a spatially non-predictive cue (i.e., 50% of the times predictive of the target’s location) emerged and was presented for 100 ms. The cue was a picture of an Archerfish, oriented either toward the left or toward the right side of the screen. After a variable stimulus onset asynchrony (SOA; 200 ms, 700 ms or 1300 ms) a target - red target asterisk - appeared for 3000 ms or until a response was detected. The target appeared at the cued location (valid) or the opposite location (invalid; as in the current example) with equal probability. After the target disappeared, a blank screen was presented between trials for 10 s. During the blank screen presentation, the fish received a food pellet for completing the spit to the target location, and the experimenter cleaned the glass shelf.

2.2. Design

Every session was composed of 24 trails, with four trials for each of the six experimental conditions (cue-target relation, valid and invalid, crossed with the 3 SOAs, 200 ms, 700 ms, & 1300 ms). Before we started to collect data, the fish were trained in the task until they achieved proficiency (training sessions lasted for about a month and resembled

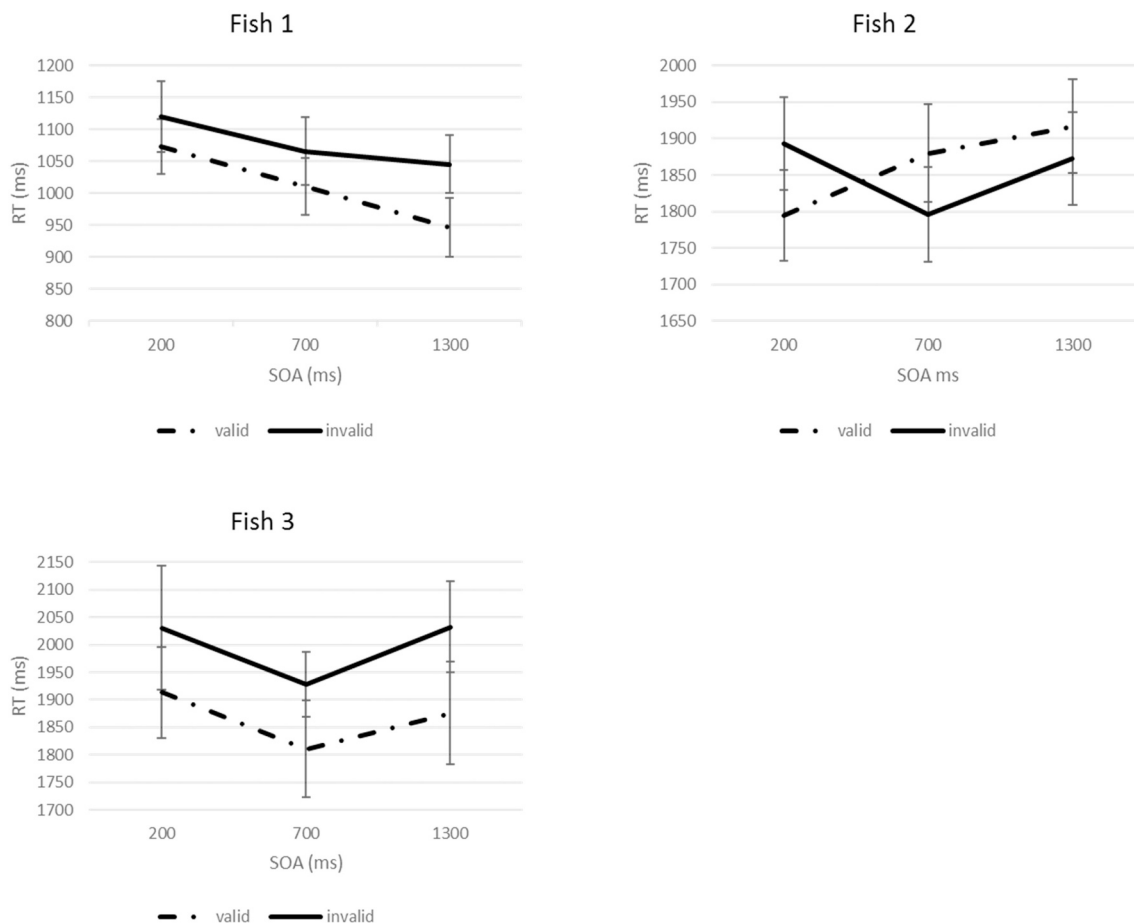


Fig. 2. Archerfish pattern of results. Sessions in which the fish responded to less than 16 out of 24 trials (responded less than ~66% of trials) and trials, in which the fish responded slowly, with reaction time (RT) longer than 2500 ms, were excluded from the analyses. Fish 1 did not respond or responded in less than 1% of the trials, Fish 2 and 3 did not respond in 22% of the trials. Fish 1 completed 32 successful sessions. Fish 2 completed 53 sessions of which 8 sessions were excluded due to low response rate. Fish 3 completed 13 sessions, 3 of them were excluded due to low response rate. RT’s as a function of SOA and Cue condition is depicted for each fish separately.

the testing sessions: one training session per day). Fish 1 completed 32 successful sessions. Fish 2 completed 53 sessions of which eight sessions were excluded due to low response rate. Fish 3 completed 13 sessions, 3 of which were excluded due to a low response rate.

3. Results

In the present study, attentional orienting as a result of non-predictive social cues was examined in three archerfish. At the shortest cue-target interval, all three fish presented an attentional bias toward the location indicated by the social cue (see Fig. 2). Two fish (1 and 3) continued to show this effect at the longer intervals while the cuing effect was not long-lasting in the third fish (#2). All fish responses were accurate and hit the target surface.

We conducted an analysis of variance (ANOVA) for each fish separately, with fixed factors of cue condition (valid vs. invalid) and SOA (200 vs. 700 vs 1300 ms), session as the random factor with RT in ms from correct trials as the dependent variable. For Fish 1, there was a statistically significant main effect of SOA ($F(2,62) = 4.38, p < .05$, partial $\eta^2 = 0.16$) which represented a decline in RT as a function of SOA length. A significant effect of the Cue condition was also observed ($F(1,31) = 5.89, p < .05$, partial $\eta^2 = 0.12$) indicating faster RT for valid compared to invalid trials. The two-way interaction was not significant. For Fish 2, although there were no significant main effects the interaction between SOA and Cue condition, was significant ($F(2,66) = 3.21, p < .05$, partial $\eta^2 = 0.09$). To further analyze this interaction, we examined the cue condition effect for each SOA separately. A significant effect of Cue condition was found only at the 200 ms SOA ($F(1,33) = 4.16, p < .05$; $F(1,33) = 1.98, n.s.$; $F(1,33) = 1.8, n.s.$; for the 200, 700, 1300 SOAs respectively). At the 200 ms SOA, the fish responded faster on valid compared to invalid trials. For fish 3, only a main effect of cue condition was observed ($F(1,9) = 5.26, p < .05$, partial $\eta^2 = 0.369$) indicating faster RT for valid compared to invalid trials.

4. Discussion

The study of gaze cuing in adult humans was stimulated by the literature on joint visual attention in infancy (for a review, see Corkum & Moore, 1998). The findings of joint attention at an early age and in different mammals suggest that this ability might have an older evolutionary origin. To explore this possibility, we adapted methods from the human literature to the archerfish. Our three fish reacted faster to targets that appeared at a socially cued location compared to targets presented at a socially un-cued location. The cues were not predictive, and hence any attentional effect elicited by them is commonly regarded as reflexive. Thus, the present study demonstrates that spatially non-predictive social attentional cues can elicit reflexive attentional shifts in the archerfish.

In human studies, the typical pattern of results when examining the time course of the cuing effects from spatially non-predictive social cues is a facilitation effect without inhibition of return (IOR; for a graphic meta-analysis, see Fig. 1. from McKee, Christie, and Klein (2007). This sensitivity to social cues is observed from infancy (Hood, Willen, & Driver, 1998), even before cortical maturation is completed (Johnson, 1990). Hietanen (2002), examining head and body orientation as social cues, demonstrated that head orientation could produce attentional shifts similar to those generated by gaze cues. The author inferred that the brain areas involved in social attention integrate information from gaze, head, and body orientation. From these findings, it is reasonable to theorize that different social cues might be relevant to different species.

In humans, the direction of gaze is more detectable than in other species due to a notable contrast between the sclera and the iris. Hence, body orientation might be a more prominent social cue in determining conspecific's attentional focus in species for which gaze is less detectable. It was previously demonstrated that the archerfish possesses reflexive attentional processes similar to humans (Gabay et al., 2013),

indicating that basic reflexive attentional processes are shared across species and can be observed even in species lacking fully developed cortical circuitry. In a follow up study it was demonstrated that the archer fish can even present attentional orienting in an endogenous attentional task (Saban et al., 2017). In the endogenous task a spatially predictive central color cue was presented and the fish learned to predict the target location according to the cue's color. At early SOAs facilitation was observed and at a longer SOA inhibition of return (IOR) emerged. This finding of IOR is in contrast to human endogenous cuing studies in which facilitation is not followed by IOR.

In the current task, a central non-predictive social cue elicited facilitation but no IOR in the archerfish, a pattern similar to that observed in humans. Because the archerfish shows IOR when presented with either an exogenous or endogenous cuing paradigm, the absence of IOR here is puzzling. One possibility is that the lack of IOR in the social cuing task in the archerfish results from the involvement of special neural substrate dedicated for processing social cues (similar to regions near the superior temporal sulcus in humans; Hoffman & Haxby, 2000); such a substrate that might not elicit IOR as an aftereffect. Another possibility is that orienting by social cues in the archerfish might have a slower and more prolonged temporal dynamic than endogenous orienting. Under this view, all attentional orienting produces IOR in the archerfish, yet orienting as a result of a social cues develops slower and is maintained for longer durations and hence delays or masks the presence of IOR. It is possible that employing longer SOAs might reveal the presence of IOR for social cues in the archerfish.

The present study has examined the attentional orienting elicited in fish by an image of a conspecific body orientation. Future studies should examine whether this tendency will only be observed for images of conspecifics or whether this will also be evident for images of other types of fish. Another interesting question that should be addressed in future studies is whether similar to some reports from humans, mental state attribution will modulate this effect (Morgan, Freeth & Smith, 2018; but see Cole, Smith & Atkinson, 2015). That is, whether the gazer's (i.e., the fish presented in the image as a social cue) view of the targets (occluded or not) will influence the effect. This might provide some insights regarding the mental world of the archerfish and whether it possesses some type of "theory of mind".

The contribution of the current study is the demonstration that social aspects of shared attention are widespread across the animal kingdom. The similarities between social attentional effects across different species suggest that the sensitivity to social cues is a ubiquitous phenomenon and therefore could have an early evolutionary origin.

5. Conclusions

The current study examined the attentional shifts of archerfish that are elicited in the gaze-cuing paradigm. We found that spatially non-predictive social attentional cues can elicit reflexive attentional shifts in the archerfish. Similarly to humans, the fish reacted faster to targets that appeared at a socially cued location even though the cues were spatially non-predictive. This behavior indicates that social aspects of shared attention are widespread across species and suggests an early evolutionary origin.

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Appendix A. Supplementary data

Supplementary data to this article can be found online at <https://doi.org/10.1016/j.cognition.2020.104511>.

References

- Cole, G. G., Smith, D. T., & Atkinson, M. A. (2015). Mental state attribution and the gaze cueing effect. *Attention, Perception, & Psychophysics*, 77(4), 1105–1115.
- Clucas, B., Marzluff, J. M., Mackovjak, D., & Palmquist, I. (2013). Do American crows pay attention to human gaze and facial expressions? *Ethology*, 119(4), 296–302. <https://doi.org/10.1111/eth.12064>.
- Corkum, V., & Moore, C. (1998). The origins of joint visual attention in infants. *Developmental psychology*, 34(1), 28.
- Davidson, G. L., Clayton, N. S., & Thornton, A. (2015). Wild jackdaws, *Corvus monedula*, recognize individual humans and may respond to gaze direction with defensive behavior. *Animal Behaviour*. <https://doi.org/10.1016/j.anbehav.2015.07.010>.
- Deaner, R. O., & Platt, M. L. (2003). Reflexive social attention in monkeys and humans. *Current Biology*, 13(18), 1609–1613. <https://doi.org/10.1016/j.cub.2003.08.025>.
- Driver, J., Davis, G., Ricciardelli, P., Kidd, P., Maxwell, E., & Baron-Cohen, S. (1999). Gaze perception triggers reflexive visuospatial orienting. *Visual Cognition*, 6(5), 509–540. <https://doi.org/10.1080/135062899394920>.
- Emery, N. J. (2000). The eyes have it: the neuroethology, function and evolution of social gaze. *Neuroscience and Biobehavioral Reviews*. [https://doi.org/10.1016/S0149-7634\(00\)00025-7](https://doi.org/10.1016/S0149-7634(00)00025-7).
- Friesen, C. K., & Kingstone, A. (1998). The eyes have it! Reflexive orienting is triggered by nonpredictive gaze. *Psychonomic Bulletin & Review*, 5(3), 490–495. <https://doi.org/10.3758/BF03208827>.
- Friesen, C. K., Moore, C., & Kingstone, A. (2005). Does gaze direction really trigger a reflexive shift of spatial attention? *Brain and Cognition*, 57(1), 66–69. <https://doi.org/10.1016/j.bandc.2004.08.025>.
- Frith, C. D., & Frith, U. (2007). Social cognition in humans. *Current Biology*, 17(16), 724–732. <https://doi.org/10.1016/j.cub.2007.05.068>.
- Gabay, S., Leibovich, T., Ben-Simon, A., Henik, A., & Segev, R. (2013). ARTICLE inhibition of return in the archer fish. *Nature Communications*, 4. <https://doi.org/10.1038/ncomms2644>.
- Ghazanfar, A. A., & Santos, L. R. (2004). Primate brains in the wild: the sensory bases for social interactions. *Nature Reviews Neuroscience*, 5(8), 603–616. <https://doi.org/10.1038/nrn1473>.
- Hare, B., & Tomasello, M. (1999). Domestic dogs (*Canis familiaris*) use human and conspecific social cues to locate hidden food. *Journal of Comparative Psychology*, 113(2), 173–177. <https://doi.org/10.1037/0735-7036.113.2.173>.
- Hietanen, J. K. (2002). Social attention orienting integrates visual information from head and body orientation. *Psychological Research*, 66(3), 174–179. <https://doi.org/10.1007/s00426-002-0091-8>.
- Hoffman, E. A., & Haxby, J. V. (2000). Distinct representations of eye gaze and identity in the distributed human neural system for face perception. *Nature Neuroscience*, 3(1), 80–84.
- Hood, B. M., Willen, J. D., & Driver, J. (1998). Adult's eyes trigger shifts of visual attention in human infants. *Psychological Science*, 9(2), 131–134.
- Johnson, M. H. (1990). Cortical maturation and the development of visual attention in early infancy. *Journal of Cognitive Neuroscience*, 2(2), 81–95.
- Kaminski, J., Riedel, J., Call, J., & Tomasello, M. (2005). Domestic goats, *Capra hircus*, follow gaze direction and use social cues in an object choice task. *Animal Behaviour*, 69(1), 11–18. <https://doi.org/10.1016/j.anbehav.2004.05.008>.
- Karoubi, N., Segev, R., & Wullimann, M. F. (2016). The brain of the archerfish *Toxotes chatareus*: a Nissl-based neuroanatomical atlas and Catecholaminergic/cholinergic systems. *Frontiers in Neuroanatomy*, 10(November), 1–20. <https://doi.org/10.3389/fnana.2016.00106>.
- Kumar, S., & Hedges, S. B. (1998). A molecular timescale for vertebrate evolution. *Nature*. <https://doi.org/10.1038/31927>.
- Langton, S. R. H., & Bruce, V. (1999). Reflexive visual orienting in response to the social attention of others. *Visual Cognition*, 6(5), 541–567. <https://doi.org/10.1080/135062899394939>.
- Morgan, E. J., Freeth, M., & Smith, D. T. (2018). Mental state attributions mediate the gaze cueing effect. *Vision*, 2(1), 11.
- McKee, D., Christie, J., & Klein, R. (2007). On the uniqueness of attentional capture by uninformative gaze cues: facilitation interacts with the Simon effect and is rarely followed by IOR. *Canadian Journal of Experimental Psychology/Revue Canadienne de Psychologie Expérimentale*, 61(4), 293–303. <https://doi.org/10.1037/cjep2007029>.
- Saban, W., Sekely, L., Klein, R. M., & Gabay, S. (2017). Endogenous orienting in the archer fish. *Proceedings of the National Academy of Sciences*, 114(29), 7577–7581.
- Schuster, S., Wöhl, S., Griebsch, M., & Klostermeier, I. (2006). Animal cognition: how archer fish learn to down rapidly moving targets. *Current Biology*, 16(4), 378–383.
- Shepherd, S. V. (2010). Following gaze: gaze-following behavior as a window into social cognition. *Frontiers in Integrative Neuroscience*, 4(March), 5. <https://doi.org/10.3389/fnint.2010.00005>.
- Tomasello, M., Hare, B., & Agnetta, B. (1999). Chimpanzees, *Pan troglodytes*, follow gaze direction geometrically. *Animal Behaviour*, 58(4), 769–777. <https://doi.org/10.1006/anie.1999.1192>.
- Werhahn, G., Sommese, A., & Range, F. (2016). Wolves (*Canis lupus*) and dogs (*Canis familiaris*) differ in following human gaze into distant space but respond similar to their Packmates' gaze. *Journal of Comparative Psychology*, 130(3), 288–298. <https://doi.org/10.1037/com0000036>.