Endogenous orienting in the archer fish

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The literature has long emphasized the neocortex's role in volitional processes. In this work, we examined endogenous orienting in an evolutionarily older species, the archer fish, which lacks neocortex-like cells. We used Posner's classic endogenous cuing task, in which a centrally presented, spatially informative cue is followed by a target. The fish responded to the target by shooting a stream of water at it. Interestingly, the fish demonstrated a human-like "volitional" facilitation effect: their reaction times to targets that appeared on the side indicated by the precue were faster than their reaction times to targets on the opposite side. The fish also exhibited inhibition of return, an aftermath of orienting that commonly emerges only in reflexive orienting tasks in human participants. We believe that this pattern demonstrates the acquisition of an arbitrary connection between spatial orienting and a nonspatial feature of a centrally presented stimulus in nonprimate species. In the literature on human attention, orienting in response to such contingencies has been strongly associated with volitional control. We discuss the implications of these results for the evolution of orienting, and for the study of volitional processes in all species, including humans.

volitional orienting | subcortical regions | endogenous orienting | IOR | attention

Humans are commonly assumed to have volitional abilities that species lacking a neocortex (e.g., fish and amphibians) do not have. The literature has long emphasized the role of cortical mechanisms in these exclusive cognitive abilities. But is a neocortex necessary for a species to manifest behaviors that have been attributed to volitional control? To examine this question, we tested whether the archer fish (*Toxotes chatareus*) is capable of endogenous orienting.

Driven by bottom-up stimulation, reflexive orienting is fast and automatic as a result of tuning through natural selection. Volitional orienting is relatively nonreflexive and is tuned to local contingencies and/or the immediate goals of the individual (1). In the current study, we adopt the typical perspective regarding spatial attention, as put forward by Posner (2), which is characterized by two distinctions: whether covert or overt adjustments are made, and whether these adjustments are under endogenous (volitional) or exogenous (reflexive) control. The most common methods for examining reflexive and volitional attentional processes are two versions of Posner's cuing task (2, 3). In this task, participants are presented with a cue followed by a peripheral target to which they are instructed to respond. Two task properties are important for determining which mode of orienting is generated. The first is whether or not the cue is informative about the location of the upcoming target, and the second is whether or not the input pathway of the upcoming target might be stimulated by the cue. When studying reflexive orienting, the peripheral location where a target might appear, or one nearby, is stimulated by a cue that is uninformative about the location of the upcoming target. When the interval [stimulus onset asynchrony (SOA)] between the cue and the target is varied, the typical pattern of results is an early facilitation of responses to targets at the cued location, followed by a later inhibitory effect (4) that has been called inhibition of return (IOR) (5, 6). When studying volitional orienting, a property of a central cue that does not stimulate the possible target locations provides information about which of the peripheral locations is more likely to contain the subsequent target. The typical pattern of results elicited in covert orienting is a gradually developing facilitation at the

cued location as the interval between the cue and the target increases. When measuring endogenous saccadic effects (overt orienting), most studies demonstrate a facilitatory effect at a wide range of SOAs (up to 1,250 ms; e.g., refs. 7–9).

It has been suggested that reflexive attention may be phylogenetically older than volitional attention (10). Consistent with this suggestion, volitional orienting is often linked to cortical regions (11–14), whereas reflexive orienting is linked to subcortical processing (15–19). Most pertinent to the present study, a recent study (20) demonstrated that the archer fish, which lacks cortical structures, shows the prototypical reflexive pattern of early facilitation followed by later IOR (20). In nature, the archer fish spits a jet of water to shoot down prey resting on foliage above the water. In an experimentally controlled environment, the archer fish can learn to respond to targets presented on a computer monitor above its tank. The finding that archer fish, a nonprimate species, have similar reflexive attentional processes, namely, facilitation and IOR (20), suggests these attentional processes in humans have an evolutionary ancestor. Fish lack laminated and columnar neural organization (21, 22), visual cortex, and frontal and parietal cortical regions (which in humans are thought to guide volitional orienting). However, the fish does possess an optic tectum, which implies that subcortical mechanisms are probably involved in these types of reflexive processes. Recently, it has been suggested that fish telencephalon is not composed mostly of basal ganglia (subpallium), but also includes pallial regions that might be homologous with the mammalian neocortex, and potentially might serve functions similar to the neocortex (23–27). However, despite these possible homologies, the fish brain has significantly less computational power than the cortices of higher organisms such as primates (28–32). As a consequence, investigation of cognitive processes in fish provides vital evidence for the complexity of the neural circuitry essential for a specific function. This is even more pronounced for cognitive abilities that have been traditionally considered to be limited to primates (e.g., volitional abilities).

Although several studies have explored attention in nonprimates, it is worth noting several features of the used tasks that limit the ability to conclude that purely endogenous attentional processes were studied. For example, in studies with rats (e.g., ref. 33) and

Significance

Volitional orienting, most commonly explored in humans using the classic Posner endogenous cuing task, is often linked to neocortical regions. We applied this task in a species lacking a neocortex (i.e., archer fish). Our study provides a demonstration of facilitation and inhibition of return as a result of a purely endogenous (centrally presented, informative, and symbolic) cue. The results have major implications for our understanding of the evolution of orienting (reflexive and volitional), and for the paradigms used to study "volitional" processes.

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chickens (e.g., ref. 34) that used a Posnerian cuing paradigm, the cues were both informative and peripheral. By combining methods used for studying endogenous (informative) and exogenous (peripheral) orienting, these studies likely generated a hybrid mode of orienting, with an indeterminate mixture of reflexive and voluntary effects (35). A methodological mixture of this kind precludes the ability to assess purely endogenous processes.

It has been known for some time that the orienting behavior of human observers can be sensitive to the information value of the properties of the scene being inspected (36). Chun and Jiang (36) referred to this as "contextual cuing," an implicitly acquired contingency between where to look and the properties of the scene. It was recently demonstrated that the orienting behavior of pigeons (37, 38), similar to that of humans, can be sensitive to the information value of the properties of a scene. In the context of the present exploration, we must note that this form of cuing is different from that explored using Posner's endogenous cuing paradigm in two important respects: the property that signals the more fruitful locus of attention is in the scene (not presented in a precue before the presentation of the target), and hence, the contextual cuing paradigm does not require the organism to maintain the information provided by the cue, and the contextual cuing paradigm has never been touted as one suitable for exploring the voluntary control of behavior.

We are not aware of any study in nonprimates that tried to generate attentional orienting using a purely endogenous (centrally presented, informative, and symbolic) cue before the presentation of a target. To fill this gap, the present experiment uses Posner's endogenous cuing task: An arbitrary, centrally presented, spatially informative cue and its ensuing peripheral target were presented to the archer fish (Fig. 1). To assess the fish endogenous orienting abilities in an ecological setting, fish were swimming freely in the tank, and the reaction time (RT) of its localization of the targets (by spitting at them) was measured. If endogenous orienting is governed by neocortical structures, then it might be predicted that lacking such structures, the archer fish will not show orienting in this purely endogenous cuing paradigm. Two SOAs were used to explore the time course of endogenous orienting (if observed) in the archer fish.

Results

Trials in which the fish responded very slowly, with RT longer than 2,500 ms, were excluded from the analyses. To explore the time-course of any orienting effects our procedures might have generated, we first conducted separate analyses of variance on the RTs of each fish (*Materials and Methods*) with the factors of SOA and validity. As illustrated in Fig. 2, each fish exhibited facilitation at the 200-ms SOA and inhibition (IOR) at the 800-ms SOA. To follow the standard analysis procedure used in conventional experiments, we also conducted a group analysis on the mean RTs for the three fish. Significant interaction between SOA and validity was observed across all fish [$F(1,2) = 33.20$; $P < 0.05$; $\eta_p^2 = 0.94$]. Follow-up simple effects tests revealed significant facilitation at the 200-ms SOA and significant IOR at the 800-ms SOA [$F(1,2) = 24.16$ ($P < 0.05$; $\eta_p^2 = 0.92$); $F(1,2) = 41.51$ ($P < 0.05$, $\eta_p^2 = 0.95$), respectively].

Discussion

Archer fish studies have focused on spitting accuracy (39–42), biomechanics of spitting (43–46), neural coding (47), and learning sensorimotor skills (48–50). In addition, a recent study also demonstrated that archer fish can learn to discriminate a large number of human face images (51). However, little is known about whether archer fish have volitional processes.

In the present study, while exploring the behavior of the archer fish during Posner's endogenous orienting attention task, we found

Fig. 1. The sequence of events in a typical experimental trial. Each trial began with the flickering of three black location markers, presented three times for 200 ms with a 600-ms interval between presentations. Six hundred milliseconds after the location markers disappeared, a red or green predictive (valid 80% of the time) cue box appeared for 100 ms at the center of the fixated location. After a variable SOA (200 ms, 800 ms), a black target asterisk appeared for 3,500 ms or until a response was detected. The target could appear at the cued location or at the opposite location (valid or invalid conditions, respectively). After the target disappeared, a blank screen was presented between trials for 10 s.
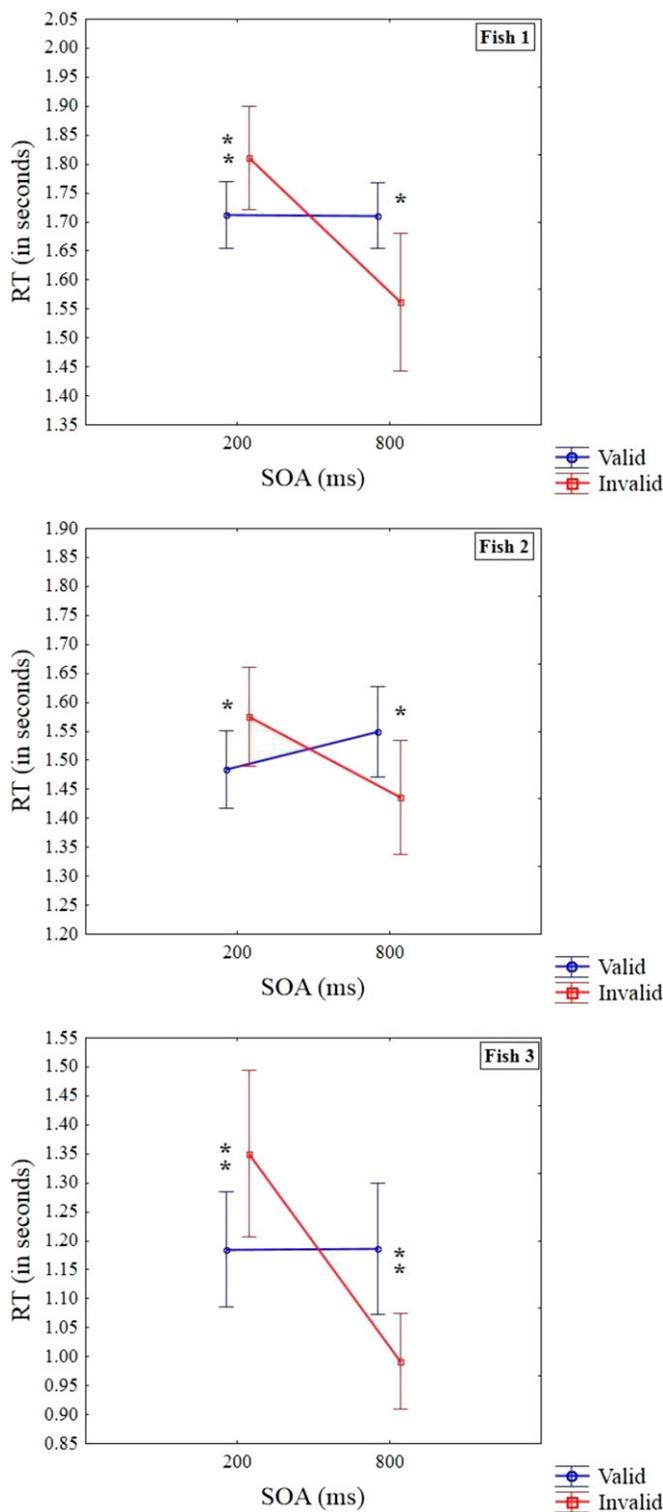
Fig. 2. RT as a function of SOA and validity for the three fish. All fish completed 21 sessions of the experiment. In an analysis of variance, a significant interaction between SOA and validity was observed in all the fish [$F_{(1,20)} = 14.29$ ($P < 0.005$; $\eta_p^2 = 0.42$); $F_{(1,20)} = 8.91$ ($P < 0.01$; $\eta_p^2 = 0.31$); and $F_{(1,20)} = 27.95$ ($P < 0.001$; $\eta_p^2 = 0.58$) for fish 1, 2, and 3, respectively]. Follow-up simple effects tests revealed the appearance of facilitation at the 200-ms SOA [$F_{(1,20)} = 8.49$ ($P < 0.01$); $F_{(1,20)} = 4.56$ ($P < 0.05$); and $F_{(1,20)} = 10.73$ ($P < 0.005$), for fish 1, 2, and 3, respectively] and IOR at the 800-ms SOA [$F_{(1, 20)} = 4.91$ ($P < 0.05$); $F_{(1,20)} = 4.79$ ($P < 0.05$); and $F_{(1,20)} = 29.33$ ($P < 0.001$), for fish 1, 2, and 3, respectively]. Ninety-five percent confidence intervals are shown in the error bars. *$P < 0.05$; **$P < 0.01$. The two functions have been slightly offset horizontally to allow visualization of the error bars.

an indication of volitional orienting. The fish were able to learn the predictable symbolic value of the cue, and their spitting RTs at the short SOA were modulated accordingly, with faster RTs at targets appearing at the cued (more probable) location. In addition to the early facilitation observed at the short SOA, the fish also demonstrated IOR at the long SOA. This is a demonstration of the appearance of an early endogenous facilitation effect that was superseded by IOR in nonhumans.

Research on voluntary attention has focused mainly on primates. The literature has emphasized the role of the cerebral cortex in volitional attentional orienting. In this study, the archer fish, a nonprimate species that lacks a neocortex, yield a result that is similar to that of humans at early SOAs (i.e., endogenous facilitation). This demonstrates that such an organism, which developed very early in evolution, can exhibit orienting behavior in a purely endogenous cuing paradigm.

In the next two sections, we explore possible explanations for the unexpected appearance of IOR at the late SOA and the implications of our finding of endogenously generated facilitation at the early SOA. By any explanation, we believe that the finding of endogenously generated facilitation has two major aspects: using the most widely accepted task (Posner's endogenous cuing paradigm) for studying volitional orienting in humans, this is a demonstration of purely endogenous orienting in a nonprimate species; and in addition to the major methodological and conceptual differences between previous studies and our task (reviewed in the *Introduction*), there are phylogenetical differences between lower vertebrates (e.g., fish) and higher ones (e.g., birds) (52–54). From an evolutionary perspective, the more than 200 million-year phylogenetic distance that separates fish from other vertebrates (e.g., humans, monkeys, and even pigeons) presents an invaluable opportunity for a comparative investigation of brain and cognition development during evolution. The current findings allow the inference that endogenous orienting and IOR are much more fundamental and primitive abilities for the survival of organisms and are shared by highly distinct species.

Inhibition of Return After an Endogenous Cue: Evolutionary Perspectives. Humans are born with a bundle of reflexes that, through ontogenetic development, come under cortical inhibitory control enabling goal-directed behavior (e.g., ref. 55). From a phylogenetic perspective, the ability to predict and to voluntarily control basic processes was developed through the evolution of the species. In addition, all living organisms are information processing systems. The information collected about the environment by each such system is used, reflexively and/or volitionally, to direct behavior.

Fish represent a taxonomic group that diverged from the other vertebrates ~450 million years ago (56). In the present study, the archer fish, a vertebrate species that is evolutionarily distant from humans, demonstrated human-like endogenous facilitation (which will be discussed in greater detail in the next section), but also presented an IOR effect, which commonly emerges in reflexive orienting tasks. Hence, the presence of IOR in an endogenous orienting task was unexpected.

It could be suggested that the fish response preparation might involve body orientation toward the predicted location, thus resulting in a shift of the fish area centralis (57) toward the attended location. Similarly, the appearance of IOR might be a result of a tendency to orient toward the uncued location at the long SOA when the target does not appear at the cued location at the short SOA. This latter possibility is improbable because at both the short and long SOAs, target probability is higher at the cued location, and hence there is no incentive for the fish to attend the uncued location at any SOA. Fish are able to learn associations across larger time spans than the one used in the current task (58, 59); therefore, it is more likely that an inhibitory process is influencing performance and producing the observed IOR pattern of results.

Two explanations for the unexpected appearance of IOR in an endogenous orienting task are discussed. Both explanations acknowledge that the archer fish demonstrated probability-appropriate

overt orienting tendencies (*Implications for the Study of Volitional Processes*) in response to the endogenous cue, which facilitate responding at the short SOA. The two explanations also recognize, as originally proposed by Posner and Cohen (4), that the inhibitory effects attributed to IOR can be present at the same time as the facilitative effects of the present locus of attention. Subsequent studies (60, 61) support this proposal and demonstrate that facilitation and inhibition might have additive effects on performance. Finally, both explanations assume that regardless of the observed underlying mechanism for early facilitation, it is transient in the archer fish and no longer operating by the time of our long SOA (800 ms after the appearance of the cue).

One explanation is based on the suggestion (62) that in human participants, endogenous preparation of overt (oculomotor) orienting is accompanied by IOR, which is overshadowed by facilitation while expectancy is maintained. The archer fish demonstrates a similar, endogenously generated overt orienting tendency. Once the archer fish (or human participant) fails to maintain the target expectancy generated by the cue, the already-present inhibitory effect is revealed. From this perspective, it might be assumed that maintaining expectancy for more than a few hundred milliseconds requires cortical control, which the archer fish lacks. This explanation is critically dependent on the observation by Rafal et al. (63) that cancellation of an endogenously generated oculomotor preparation is followed by IOR (63). As Chica et al. (64) were unable, in successive attempts, to replicate this critical finding reported by Rafal et al. (63), we do not favor this explanation.

We prefer the simpler alternative explanation in which IOR is generated primarily by subcortical structures (5, 17, 65), and in primates, it may be modulated by cortical regions (15, 66). In line with previous research (25), in fish, spatial learning is dependent on the pallium region, and it is plausible that the fish telencephalon contributes to endogenous orienting. However, in contrast to primates' neocortical control, pallial influence over the optic tectum might be insufficient to inhibit IOR generated by the preparation of an overt orienting response.

Accordingly, it has recently been suggested that in primates, the primary visual cortex (V1) creates a saliency map of the visual world (67). In lower vertebrates, such as fish, V1 is absent and the superior colliculus (which is called the optic tectum in lower vertebrates) receives retinal input. Hence, it is possible that through evolution, this saliency map of the visual world migrated from the optic tectum to the V1. It has been suggested (67) that reflexive cuing effects observed in humans should also be present in lower vertebrates. Therefore, it is possible that when attention is guided by a saliency map at the optic tectum (as in fish), IOR (which is a reflexive attentional process guided by the optic tectum) is activated in both modes of orienting (exogenous and endogenous). As a consequence, we recommend conducting neuroscientific studies of the archer fish and of humans performing our task to test these possibilities.

Implications for the Study of Volitional Processes. The present study has important implications for conceptual understanding of volitional control processes and their operationalization in cognitive sciences. To explore these issues, it will be helpful if, in contrast to the common conflation of the terms "endogenous" and "voluntary," we explicitly distinguish between them, using "endogenous" to refer to the combination of methods used and "voluntary" to refer to a conceptual attribution. As described in the introduction and used in the present study, perhaps the most common method for exploring the voluntary control of orienting is Posner's endogenous cuing paradigm.

One possible interpretation of our finding of facilitation in the archer fish shortly after a centrally presented, informative cue is that the archer fish is demonstrating voluntary control. For those who find this implausible because of the limited cortical circuitry in this species, or for other reasons, we offer a plausible alternative. We propose that the archer fish has learned the conditional contingency between the cue's color and the later target's location.

This learning process generates activation of the conditionally probable orienting response, which accelerates the correct response on valid trials. This account, in terms of conditional discrimination learning, coincides with a recent study of human performance (68), suggesting that implicit learning of cue-target contingencies plays a role in the magnitude of endogenous cueing effects when the validity of the cue is manipulated.

Researchers interested in the volitional control of behavior need to be aware of the fact that probability manipulation, which is inherent in the endogenous cuing paradigm pioneered by Posner, allows for cuing effects that are implicitly acquired, and therefore may not reflect volitional control. Researchers who use this paradigm are therefore obliged to obtain converging evidence from other paradigms that are not subject to the possibility of associative learning.

Conclusion

The present study provides a demonstration of facilitation and IOR as a result of a purely endogenous (central, informative, and symbolic) cue in a species lacking a neocortex. As we have discussed, the results may have major implications for our understanding of the evolutionary development of orienting processes (facilitation and IOR) and for the paradigms used to study volitional control processes in all species, including humans.

Materials and 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, individually, three archer fish in a specially arranged tank, as described here. Each fish was swimming freely in the water tank during the task. A 21-inch Samsung LCD monitor (model S24C650PL) was placed on a glass shelf 41 cm above water level. The fish were trained to shoot at the target stimuli and were recorded using a GigE Camera color (120 fps 640 × 480 1/4). RT was calculated by measuring the time from target appearance until the fish's shooting onset. Successful shots were determined when the water jet landed on the surface of the target. After each successful shot, the fish received a pellet of food and the experimenter cleaned the water from the glass shelf. The cue was predictive regarding target location; that is, the target appeared at the predicted location in 80% of the trials.

In each session, each fish performed 40 trials (32 valid and 8 invalid), composed of two different SOAs (200 ms or 800 ms) and two validity conditions (valid and invalid). Before we started to collect data, the fish were trained in the task until they achieved proficiency (training sessions were similar to the testing sessions: five sessions for each fish separately, one training session per day). Each trial began with the flickering of three black location markers (4.2° height and 6.95° width), with centers positioned 8.3° from each other. Flickering was achieved by flashing the three location markers three times (i.e., they appeared for 200 ms at a time with a 600-ms interval between appearances). One thousand two hundred milliseconds after the location markers disappeared, a red (predicting a target to the left of the cued box) or green (predicting a target to the right of the cued box) cue box (4.2° in height and 6.95° in width) appeared for 100 ms at the center of the screen. After a variable SOA (200 or 800 ms), a black target asterisk (2.1° in height and 2.8° in width) appeared for 3,500 ms or until a response was detected. The target could appear at the cued location or at the opposite location. After the target disappeared, a blank interval screen was presented between trials for 10 s. After the training period, we ran each fish through the task for a period of about 2 mo. Each fish performed 21 sessions, and each session included 40 trials, so that overall, each fish had 840 experimental trials. In general, at the beginning of each trial and during cue presentation, the fish swam close to the water level and was relatively still awaiting target presentation. When the target was presented, the fish initiated its response by elevating its mouth above water level and shooting a stream of water on the target stimuli (Movie S1). The fish made no anticipatory errors and did not respond to the cued location on invalid trials. The target was the only stimulus presented long enough for the fish to respond. When responses were initiated, all fish were 100% accurate in all conditions. The percentage of trials in which the fish did not respond to target appearance in each condition is: valid, 200 ms SOA, 12.5; valid, 800 ms SOA, 8.8; invalid, 200 ms SOA, 8.3; invalid, 800 ms SOA, 9.1; and no significant effects were observed at each SOA ($P > 0.1$). In every session, the average RT was computed for each experimental condition: valid 200 ms SOA, valid 800 ms SOA, invalid 200 ms SOA, and invalid 800 ms SOA.

1. Klein RM, Lawrence MA (2012) On the modes and domains of attention. *Cognitive Neuroscience of Attention*, ed Posner MI (Guilford Press, New York), 2nd Ed, pp 11–28.
2. Posner MI (1980) Orienting of attention. *Q J Exp Psychol* 32:3–25.
3. Klein RM (2005) On the role of endogenous orienting in the inhibitory aftermath of exogenous orienting. *Developing individuality in the human brain: A tribute to Michael Posner*, eds Mayr U, Awh E, Keele S (American Psychological Association, Washington, DC), pp 45–64.
4. Posner MI, Cohen Y (1984) Components of visual orienting. *Atten Perform X Control Lang Process* 32:531–556.
5. Posner MI, Rafal RD, Choate LS, Vaughan J (1985) Inhibition of return: Neural basis and function. *Cogn Neuropsychol* 2:211–228.
6. Klein RM (2000) Inhibition of return. *Trends Cogn Sci* 4:138–147.
7. Henik A, Rafal R, Rhodes D (1994) Endogenously generated and visually guided saccades after lesions of the human frontal eye fields. *J Cogn Neurosci* 6:400–411.
8. Hodgson TL, Muller HJ (1999) Attentional orienting in two-dimensional space. *Q J Exp Psychol Sect A* 52:615–648.
9. Posner MI, Nissen MJ, Ogden WC (1978) Attended and unattended processing modes: The role of set for spatial location. *Modes of Perceiving and Processing Information* (Erlbaum, Hillsdale, NJ), pp 137–157.
10. Carrasco M (2011) Visual attention: The past 25 years. *Vision Res* 51:1484–1525.
11. Corbetta M, Kincade JM, Ollinger JM, McAvoy MP, Shulman GL (2000) Voluntary orienting is dissociated from target detection in human posterior parietal cortex. *Nat Neurosci* 3:292–297.
12. Kincade JM, Abrams RA, Astafiev SV, Shulman GL, Corbetta M (2005) An event-related functional magnetic resonance imaging study of voluntary and stimulus-driven orienting of attention. *J Neurosci* 25:4593–4604.
13. Peelen MV, Heslenfeld DJ, Theeuwes J (2004) Endogenous and exogenous attention shifts are mediated by the same large-scale neural network. *Neuroimage* 22:822–830.
14. Rosen AC, et al. (1999) Neural basis of endogenous and exogenous spatial orienting. A functional MRI study. *J Cogn Neurosci* 11:135–152.
15. Dorris MC, Klein RM, Everling S, Munoz DP (2002) Contribution of the primate superior colliculus to inhibition of return. *J Cogn Neurosci* 14:1256–1263.
16. Gabay S, Behrmann M (2014) Attentional dynamics mediated by subcortical mechanisms. *Atten Percept Psychophys* 76:2375–2388.
17. Sapir A, Soroker N, Berger A, Henik A (1999) Inhibition of return in spatial attention: Direct evidence for collicular generation. *Nat Neurosci* 2:1053–1054.
18. Self MW, Roelfsema PR (2010) A monocular, unconscious form of visual attention. *J Vis* 10:1–23.
19. Zackon DH, Casson EJ, Zafar A, Stelmach L, Racette L (1999) The temporal order judgment paradigm: Subcortical attentional contribution under exogenous and endogenous cueing conditions. *Neuropsychologia* 37:511–520.
20. Gabay S, Leibovich T, Ben-Simon A, Henik A, Segev R (2013) Inhibition of return in the archer fish. *Nat Commun* 4:1657.
21. Wullimann MF (1997) The central nervous system. *The Physiology of Fishes*, ed Evans DH (CRC Press LLC, New York), pp 245–281.
22. Northcutt RG (2011) Do teleost fishes possess a homolog of mammalian isocortex? *Brain Behav Evol* 78:136–138.
23. Wullimann MF, Mueller T (2004) Teleostean and mammalian forebrains contrasted: Evidence from genes to behavior. *J Comp Neurol* 475:143–162.
24. Jarvis ED, et al.; Avian Brain Nomenclature Consortium (2005) Avian brains and a new understanding of vertebrate brain evolution. *Nat Rev Neurosci* 6:151–159.
25. Portavella M, Vargas JP (2005) Emotional and spatial learning in goldfish is dependent on different telencephalic pallial systems. *Eur J Neurosci* 21:2800–2806.
26. Rodríguez JP, et al. (2006) Trade-offs across space, time, and ecosystem services. *Ecol Soc* 11:28.
27. Costa SS, et al. (2011) Sex differences in the dorsolateral telencephalon correlate with home range size in blenniid fish. *Brain Behav Evol* 77:55–64.
28. Van Essen DC, Anderson CH, Felleman DJ (1992) Information processing in the primate visual system: An integrated systems perspective. *Science* 255:419–423.
29. Hansel D, Sompolinsky H (1996) Chaos and synchrony in a model of a hypercolumn in visual cortex. *J Comput Neurosci* 3:7–34.
30. Kawai H, Arata N, Nakayasu H (2001) Three-dimensional distribution of astrocytes in zebrafish spinal cord. *Glia* 36:406–413.
31. Hill A, Howard CV, Strahle U, Cossins A (2003) Neurodevelopmental defects in zebrafish (Danio rerio) at environmentally relevant dioxin (TCDD) concentrations. *Toxicol Sci* 76:392–399.
32. Horton JC, Adams DL (2005) The cortical column: A structure without a function. *Philos Trans R Soc Lond B Biol Sci* 360:837–862.
33. Marote CF, Xavier GF (2011) Endogenous-like orienting of visual attention in rats. *Anim Cogn* 14:535–544.
34. Sridharan D, Ramamurthy DL, Schwarz JS, Knudsen EI (2014) Visuospatial selective attention in chickens. *Proc Natl Acad Sci USA* 111:E2056–E2065.
35. Klein R (2009) On the control of attention. *Can J Exp Psychol* 63:240.
36. Chun MM, Jiang Y (1998) Contextual cueing: Implicit learning and memory of visual context guides spatial attention. *Cognit Psychol* 36:28–71.
37. Wasserman EA, Teng Y, Castro L (2014) Pigeons exhibit contextual cueing to both simple and complex backgrounds. *Behav Processes* 104:44–52.
38. Wasserman EA, Teng Y, Brooks DI (2014) Scene-based contextual cueing in pigeons. *J Exp Psychol Anim Learn Cogn* 40:401–418.
39. Herald ES (1956) How accurate is the archer fish? *Pac Discovery* 9:12–13.
40. Bekoff M, Dorr R (1976) Predation by "shooting" in archer fish, Toxotes jaculatrix: Accuracy and sequences. *Bull Psychon Soc* 7:167–168.
41. Timmermans P, Ja (2000) Prey catching in the archer fish: Marksmanship, and endurance of squirting at an aerial target. *Neth J Zool* 50:411–423.
42. Timmermans PJ (2001) Prey catching in the archer fish: Angles and probability of hitting an aerial target. *Behav Processes* 55:93–105.
43. Myers GS (1952) How the shooting apparatus of the archer fish was discovered. *Aquarium J* 23:210–214.
44. Lüling KH (1958) Morphologisch-anatomische und histologische untersuchungen am auge des schützenfisches Toxotes jaculatrix (Pallas 1766) (Toxotidae), nebst bemerkungen zum spuckgehaben. *Zoomorphology* 47:529–610.
45. Milburn O, Alexander R (1976) The performance of the muscles involved in spitting by the archerfish Toxotes. *J Zool* 180:243–251.
46. Elshoud GCA, Koomen P (1985) A biomechanical analysis of spitting in archer fishes (Pisces, Perciformes, Toxidae). *Zoomorphology* 105:240–252.
47. Segev R, Schneidman E, Goodhouse J, Berry MJ, 2nd (2007) Role of eye movements in the retinal code for a size discrimination task. *J Neurophysiol* 98:1380–1391.
48. Timmermans PJ, Vossen JM (2000) Prey catching in the archer fish: Does the fish use a learned correction for refraction? *Behav Processes* 52:21–34.
49. Schuster S, Rossel S, Schmidtmann A, Jäger I, Poralla J (2004) Archer fish learn to compensate for complex optical distortions to determine the absolute size of their aerial prey. *Curr Biol* 14:1565–1568.
50. Schuster S, Wöhl S, Griebsch M, Klostermeier I (2006) Animal cognition: How archer fish learn to down rapidly moving targets. *Curr Biol* 16:378–383.
51. Newport C, Wallis G, Reshitnyk Y, Siebeck UE (2016) Discrimination of human faces by archerfish (Toxotes chatareus). *Sci Rep* 6:27523.
52. Jerison HJ (1973) *Evolution of the Brain and Intelligence* (Academic Press, New York).
53. Zoccolan D, Cox DD, Benucci A (2015) Editorial: What can simple brains teach us about how vision works. *Front Neural Circuits* 9:51.
54. Rosa Salva O, Sovrano VA, Vallortigara G (2014) What can fish brains tell us about visual perception? *Front Neural Circuits* 2014;8:119.
55. Rafal R, Henik A (1994) The neurology of inhibition: Integrating controlled and automatic processes. *Inhibitory Processes in Attention, Memory and Language*, eds Dagenbach D, Carr T (Academic Press, San Diego), pp 1–50.
56. Kumar S, Hedges SB (1998) A molecular timescale for vertebrate evolution. *Nature* 392:917–920.
57. Ben-simon A, Ben-shahar O (2017) Visual acuity in the archerfish: Behavior, anatomy, and neurophysiology. *J Vis* 12:1–19.
58. Hughes RN, Blight CM (1999) Algorithmic behaviour and spatial memory are used by two intertidal fish species to solve the radial maze. *Anim Behav* 58:601–613.
59. Portavella M, Torres B, Salas C (2004) Avoidance response in goldfish: Emotional and temporal involvement of medial and lateral telencephalic pallium. *J Neurosci* 24:2335–2342.
60. Berger A, Henik A, Rafal R (2005) Competition between endogenous and exogenous orienting of visual attention. *J Exp Psychol Gen* 134:207–221.
61. Berlucchi G, Chelazzi L, Tassinari G (2000) Volitional covert orienting to a peripheral cue slows down cue-induced inhibition of return. *J Cogn Neurosci* 12:648–663.
62. Rafal R, Machado L, Ro T, Ingle H (2000) Looking forward to looking: Saccade preparation and control of the visual grasp reflex. *Control of Cognitive Operations: Attention and Performance XVIII*, eds Monsell S, Driver J (MIT Press, Cambridge, MA), pp 155–174.
63. Rafal RD, Calabresi PA, Brennan CW, Sciolto TK (1989) Saccade preparation inhibits reorienting to recently attended locations. *J Exp Psychol Hum Percept Perform* 15:673–685.
64. Chica AB, Klein RM, Rafal RD, Hopfinger JB (2010) Endogenous saccade preparation does not produce inhibition of return: Failure to replicate Rafal, Calabresi, Brennan, & Sciolto (1989). *J Exp Psychol Hum Percept Perform* 36:1193–1206.
65. Klein RM, Hilchey MD (2011) Oculomotor inhibition of return. *The Oxford Handbook of Eye Movements*, eds Liversedge S, Gilchrist I, Everling S (Oxford University Press, Oxford, United Kingdom), pp 471–492.
66. Behrmann M, Zemel RS, Mozer MC (1998) Object-based attention and occlusion: Evidence from normal participants and a computational model. *J Exp Psychol Hum Percept Perform* 24:1011–1036.
67. Zhaoping L (2016) From the optic tectum to the primary visual cortex: Migration through evolution of the saliency map for exogenous attentional guidance. *Curr Opin Neurobiol* 40:94–102.
68. Risko EF, Stolz JA (2010) The proportion valid effect in covert orienting: Strategic control or implicit learning? *Conscious Cogn* 19:432–442.

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