Appendix 1:

Dynamic Programming Equations

Balancing sampling and specialization:

An adaptationist model of incremental development

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State variables

$X_0(t) \equiv$ the number of cues sampled indicating a *world–0* at time t

$X_1(t) \equiv$ the number of cues sampled indicating a *world–1* at time t

$Y_0(t) \equiv$ the number of steps towards the *world–0* phenotype at time t

$Y_1(t) \equiv$ the number of steps towards the *world–1* phenotype at time t

Where t denotes the current time period. The organism makes decisions in time period 1 to time period 20. T denotes the end of development, $t = 21$.

For a given time period t, these state variables take on the values x_0, x_1, y_0, y_1.

Parameters

$P(w_0) \equiv$ the probability of being born into *world–0* across evolutionary time

$P(w_1) \equiv$ the probability of being born into *world–1* across evolutionary time

$$P(w_0) + P(w_1) = 1$$

$P(c_0|w_0) \equiv$ the probability of a cue indicating *world–0* when in *world–0*

$P(c_1|w_1) \equiv$ the probability of a cue indicating *world–1* when in *world–1*

$$P(c_0|w_0) + P(c_1|w_0) = 1$$
$$P(c_1|w_1) + P(c_0|w_1) = 1$$

We assume that these cue validities are symmetric in the following way:

$$P(c_0|w_0) = P(c_1|w_1)$$

Posterior beliefs

After each cue sampled, the organism updates its belief about the state of the world. These beliefs are computed by Bayes' theorem, using the evolutionary prior probabilities $\{P(w_0), P(w_1)\}$, the cue validities $\{P(c_0|w_0), P(c_1|w_1)\}$, and the set of cues the organism has sampled thus far $\{x_0, x_1\}$.

Letting *D* denote the set of cues sampled, where $D = \{x_0, x_1\}$, we can compute the probability of observing this set of cues:

$$P(D) = P(D|w_0)P(w_0) + P(D|w_1)P(w_1)$$

We can compute the probabilities of obtaining D in either *world–0* or *world–1* by:

$$\begin{aligned} P(D|w_0) &= \binom{x_0 + x_1}{x_0} P(c_0|w_0)^{x_0} P(c_1|w_0)^{x_1} \\ P(D|w_1) &= \binom{x_0 + x_1}{x_0} P(c_1|w_1)^{x_1} P(c_0|w_1)^{x_0} \end{aligned}$$

Next, we denote the posterior beliefs, which will be functions of the sampled cues:

$b_0(D) \equiv$ the posterior belief of being in *world–0*

$b_1(D) \equiv$ the posterior belief of being in *world–1*

Because there are only two states of the world, the organism's beliefs in these two states must sum to one, $b_0(D) + b_1(D) = 1$.

Using Bayes' theorem, we can compute these posterior beliefs:

$$b_0(D) = \frac{P(D|w_0)P(w_0)}{P(D|w_0)P(w_0) + P(D|w_1)P(w_1)}$$

$$b_1(D) = \frac{P(D|w_1)P(w_1)}{P(D|w_0)P(w_0) + P(D|w_1)P(w_1)}$$

Fitness of mature phentoypes

The developing organism makes decisions to sample or specialize in each time period. There are no fitness consequences to these decisions *during* development. Instead, fitness is accrued *after* development, determined by the correspondence between the mature phenotype and environmental state.

Let $\phi(x_0, x_1, y_0, y_1)$ denote the expected lifetime fitness of a mature organism, having sampled a set of cues $\{x_0, x_1\}$ and developed a phenotype $\{y_0, y_1\}$.

The expected lifetime fitness (ϕ) is the sum of two products: the probability of being in *world–0* (b_0) multiplied by the fitness associated with the realized *world–0* phenotype (y_0), added to the probability of being in a *world–1* (b_1) multiplied by the fitness associated with the realized *world–1* phenotype (y_1).

The function specifying how degree of phenotypic specialization translates into fitness can take one of three forms: linear, diminishing, and increasing.

Linear returns

$$\phi(x_0, x_1, y_0, y_1) = b_0\ y_0 + b_1\ y_1$$

The maximum fitness is $T - 1 = 20$, as there are 20 developmental decisions.

Diminishing returns

$$\phi(x_0, x_1, y_0, y_1) = b_0\ \alpha(1 - e^{-\beta y_0}) + b_1\ \alpha(1 - e^{-\beta y_1})$$

We set β = 0.2, where β determines the deceleration of the curve. To ensure that the maximum fitness is 20, we set $\alpha = \frac{T-1}{1-e^{-\beta(T-1)}}$.

Increasing returns

$$\phi(x_0, x_1, y_0, y_1) = b_0\ \alpha(e^{\beta y_0} - 1) + b_1\ \alpha(e^{\beta y_1} - 1)$$

We set β = 0.2, where β determines the acceleration of the curve. To ensure that the maximum fitness is 20, we set $\alpha = \frac{T-1}{e^{\beta(T-1)}-1}$.

Decisions during development

In all time periods, except the last one (T), the organism chooses between three options: sample a cue to the state of the world, specialize one increment toward the *world–0* phenotype, or specialize one increment toward the *world–1* phenotype.

The organism chooses the option with the highest expected fitness. In the event of a tie between two or three choices, the organism chooses amongst the alternative optimal choices with equal probability.

Whereas choosing to specialize toward a phenotypic target occurs with certainty, choosing to sample a cue to the state of the world can result in one of two outcomes (c_0 or c_1) depending on the belief of being in *world–0*. Because $b_0(D) + b_1(D) = 1$, we only need to track one posterior belief.

$P_s(c_0) \equiv$ the probability of sampling a cue to *world–0* if the organism samples

$P_s(c_1) \equiv$ the probability of sampling a cue to *world–1* if the organism samples

$$P_s(c_o) = P(c_o|w_o)\; b_0 + P(c_o|w_1)\; b_1$$
$$P_s(c_1) = P(c_1|w_o)\; b_0 + P(c_1|w_1)\; b_1$$

Let $F(x_0, x_1, y_0, y_1, t)$ denote the maximum expected value of the lifetime fitness function based on decisions made between time period t and T, when the organism has thus far sampled cues $\{x_0, x_1\}$ and a phenotype $\{y_0, y_1\}$.

$$F(x_0, x_1, y_0, y_1, t) = \\ \max E\left\{ \phi\big(X_0(T), X_1(T), Y_0(T), Y_1(T)\big) \middle| \begin{array}{l} X_0(t) = x_0 \\ X_1(t) = x_1 \\ Y_0(t) = y_0 \\ Y_1(t) = y_1 \end{array} \right\}$$

After development, in time period T, the fitness of the mature organism will be:

$$F(x_0, x_1, y_0, y_1, T) = \phi(x_0, x_1, y_0, y_1)$$

In each time period during development ($t < T$), the organism makes the optimal decision (i.e., the decision that maximizes expected lifetime fitness). The fitnesses associated with each choice in time period t are denoted by:

$$F_0(x_0, x_1, y_0, y_1, t) = F(x_0, x_1, y_0 + 1, y_1, t + 1)$$

$$F_1(x_0, x_1, y_0, y_1, t) = F(x_0, x_1, y_0, y_1 + 1, t + 1)$$

$$E\big[F_s(x_0, x_1, y_0, y_1, t)\big] = \begin{array}{l} P_s(c_o)F(x_0 + 1, x_1, y_0, y_1, t + 1) + \\ P_s(c_1)F(x_0, x_1 + 1, y_0, y_1, t + 1) \end{array}$$

The expected fitness for a given state is the expected fitness associated with the choice resulting in the highest expected lifetime fitness:

$$F(x_0, x_1, y_0, y_1, t) = \max \begin{bmatrix} F_0 \\ F_1 \\ E[F_s] \end{bmatrix}$$

Appendix 2:

Optimal Developmental Programs

* In the article, we present the optimal developmental programs when the evolutionary prior probability of each world is 0.5 (Figure 2). Here, we present the optimal developmental programs for priors of 0.7 and 0.9.

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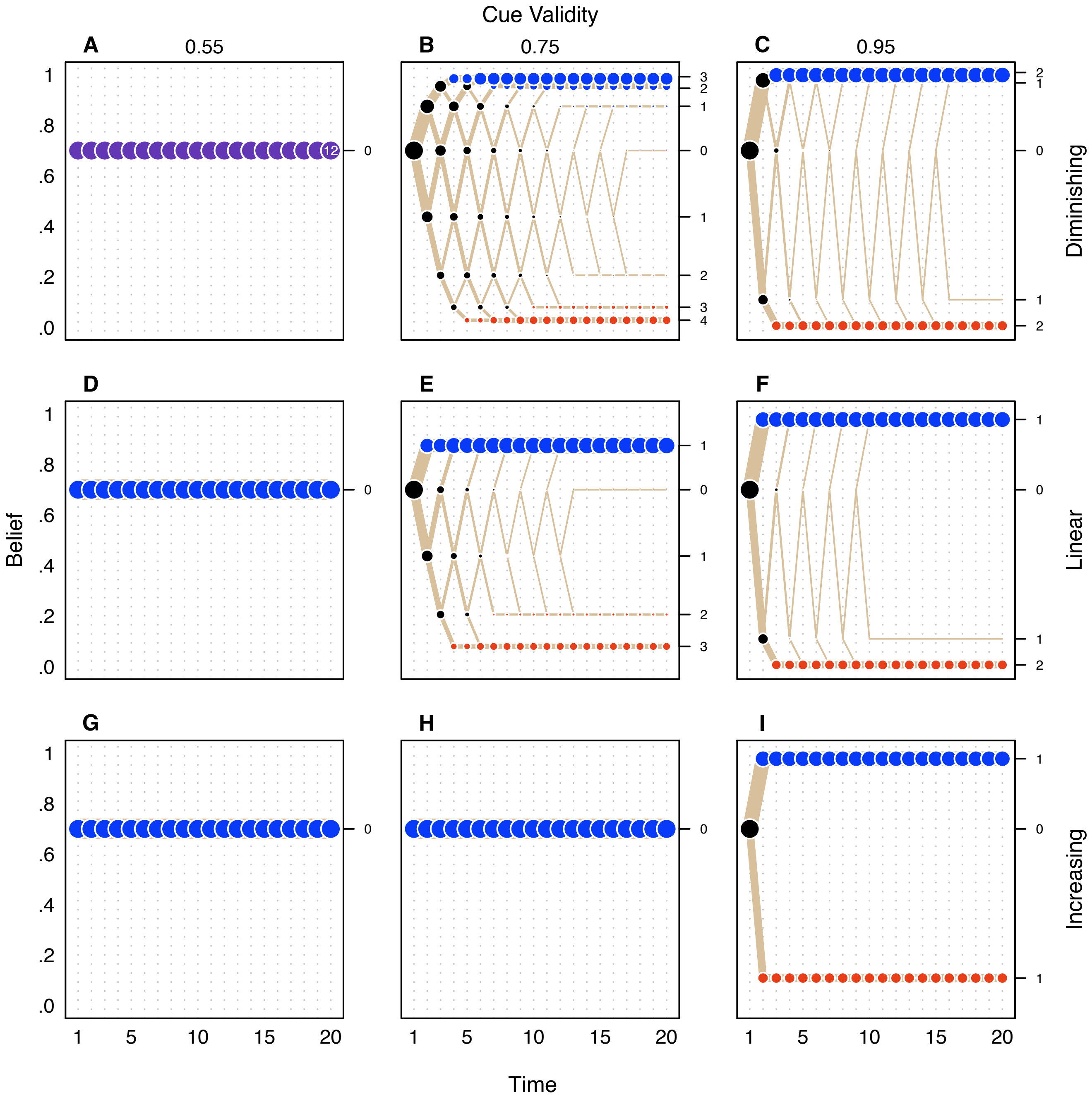
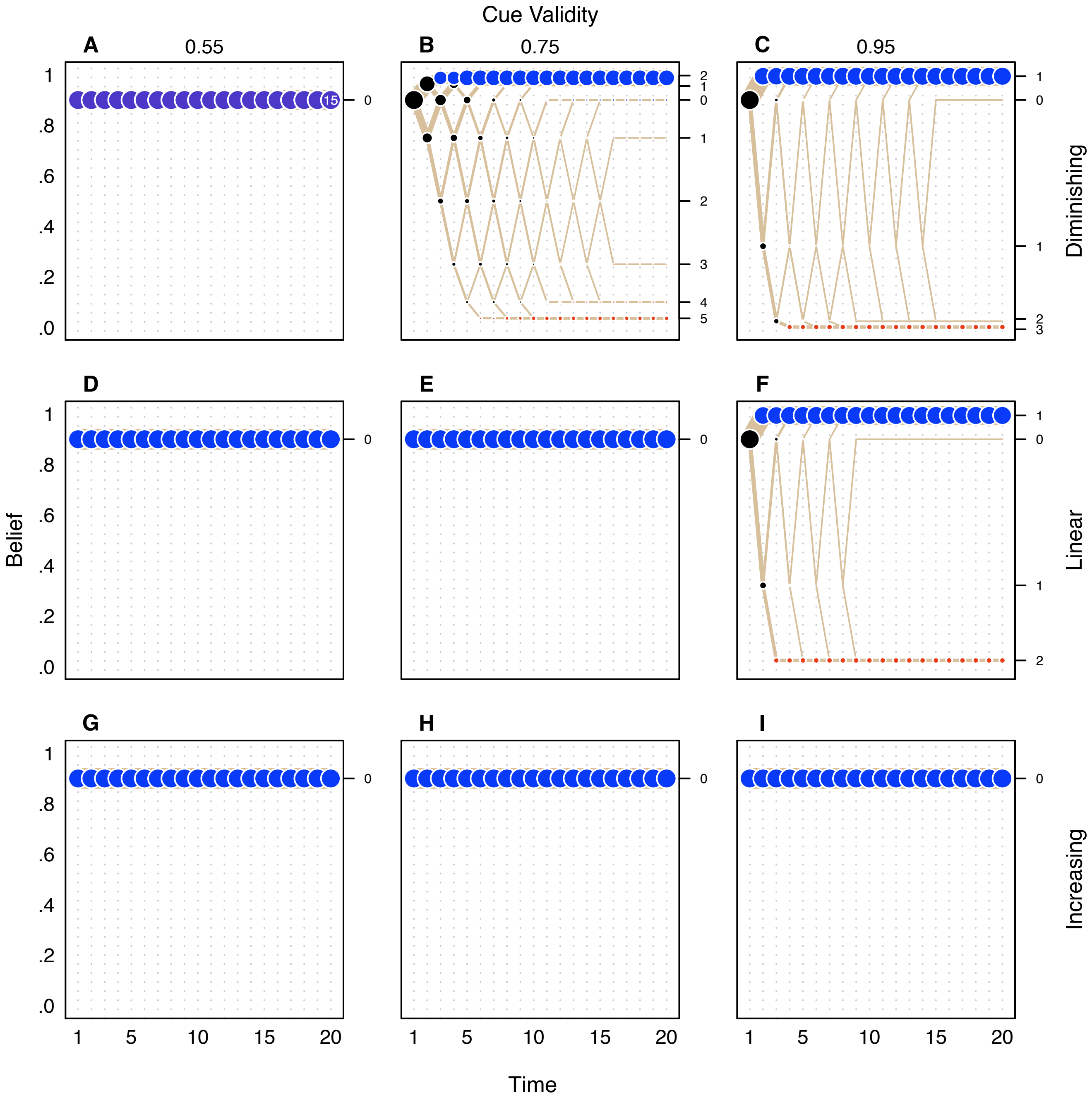


Cue Validity
A
0.55
B
0.75
C
0.95
D
E
F
G
H
I
Belief
Time
Diminishing
Linear
Increasing
1
.8
.6
.4
.2
.0
1
5
10
15
20
12


Cue Validity
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0.55
B
0.75
C
0.95
D
E
F
G
H
I
Belief
Time
Diminishing
Linear
Increasing
1
.8
.6
.4
.2
.0
1
5
10
15
20
15
0
1
2
3
4
5

Appendix 3:
Distributions of Phenotypes

* In the article, we present the distributions of phenotypes when the evolutionary prior probability of each world is 0.5 (Figure 3). Here, we present the distributions for priors of 0.1, 0.3, 0.7 and 0.9.

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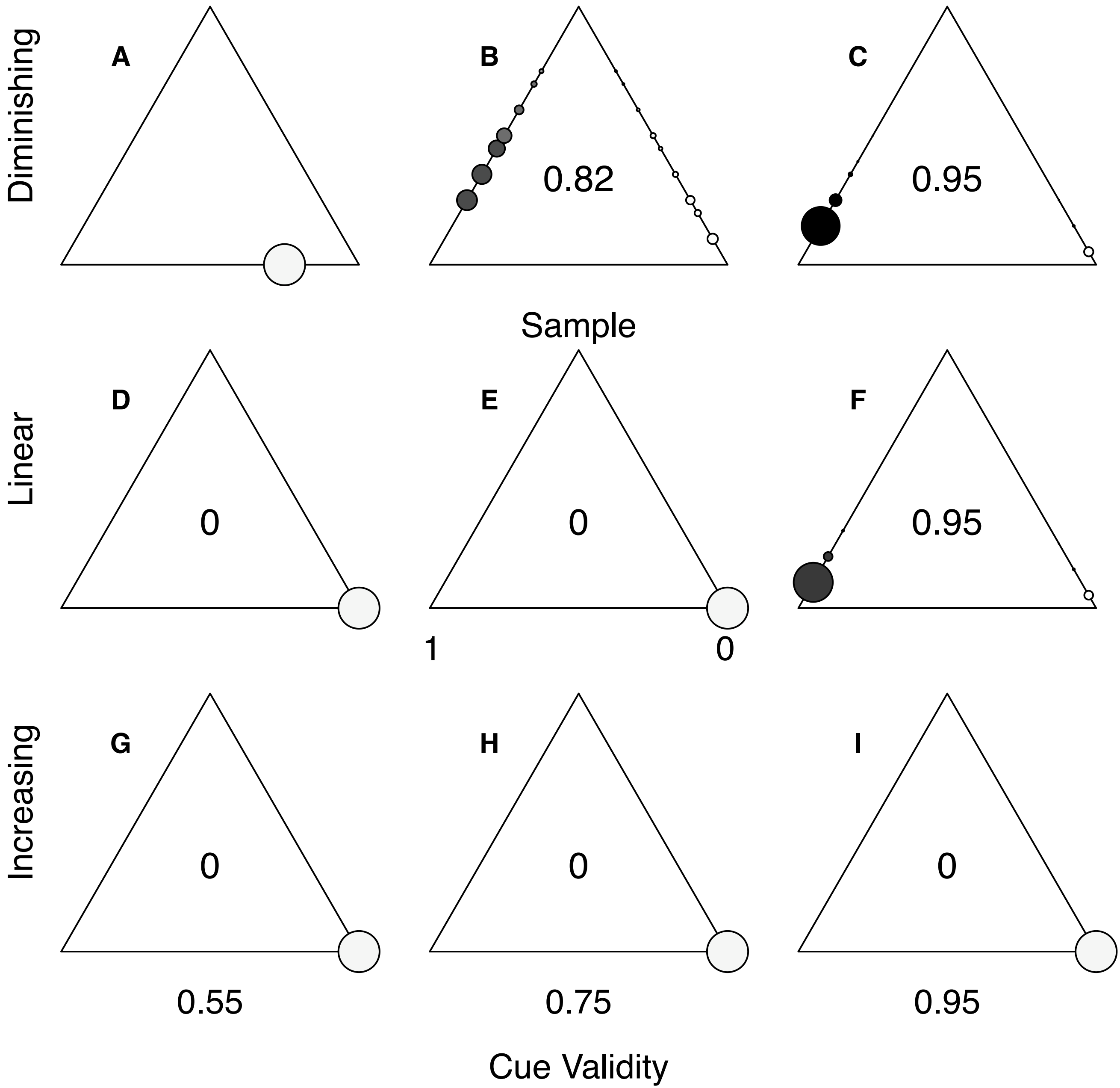

Diminishing
Linear
Increasing
A
B
C
D
E
F
G
H
I
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0.95
0
0
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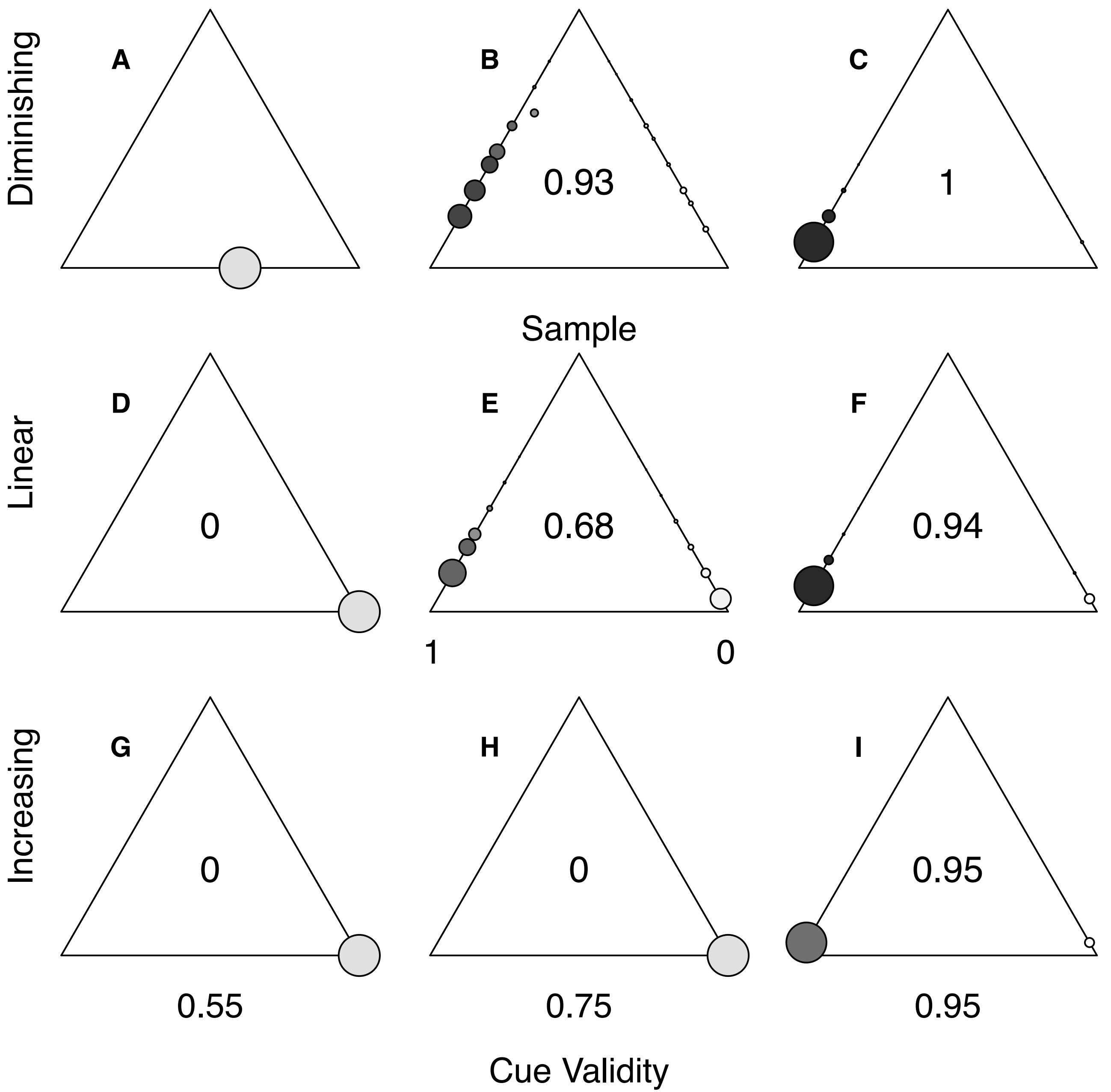
0
0
0
Sample
1
0
0.55
0.75
0.95
Cue Validity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Increasing
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B
C
D
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G
H
I
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0
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Sample
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0
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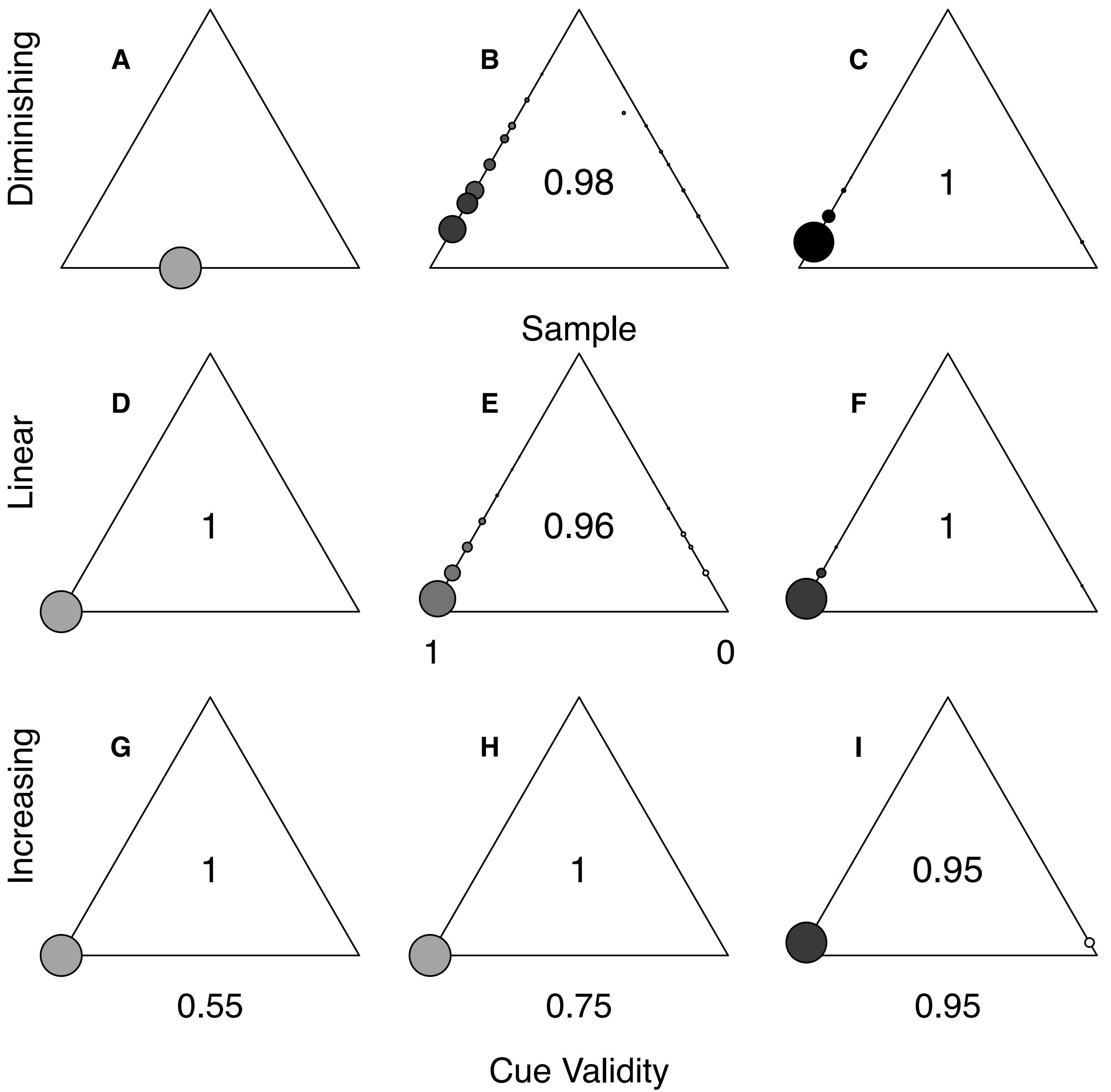
0.75
0.95
Cue Validity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Increasing
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F
G
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0
1
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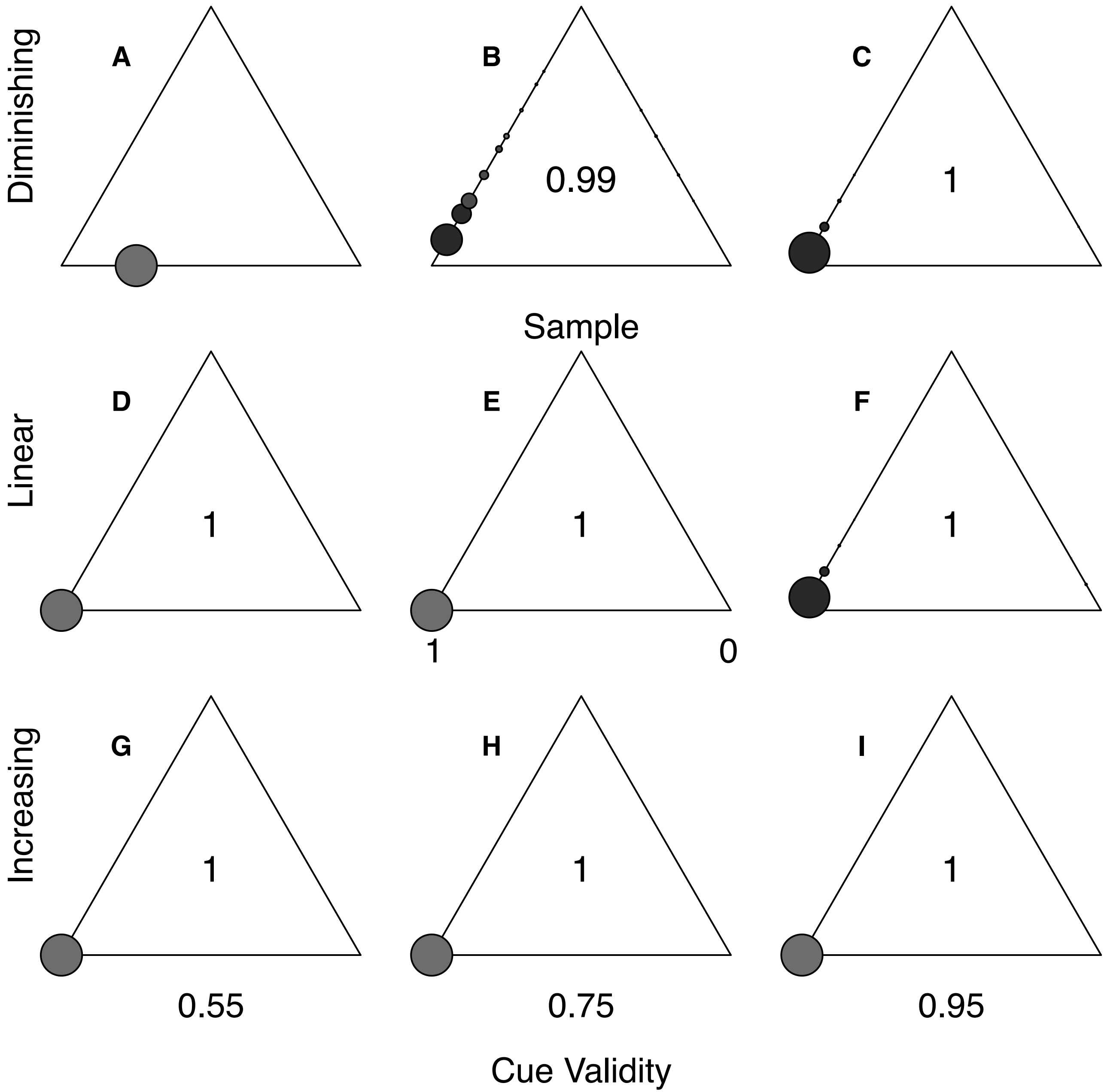
0.95
0.55
0.75
0.95
Cue Validity



Diminishing
Linear
Increasing
A
B
C
D
E
F
G
H
I
0.99
1
1
1
1
1
1
1
Sample
1
0
0.55
0.75
0.95
Cue Validity