Toward the neural causes of human visual perception and behavior

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Outline

- Neural correlates of perception
  - **Exp. 1**: Alpha oscillation as a clock signal for visual processing
- From neural correlates to neural causes of perception: decoded neurofeedback as a tool to study causality
  - **Exp. 2**: Creation of color perception by manipulation of neural activity in the primary and secondary visual areas
  - **Exp. 3**: Change in perceptual confidence by manipulation of neural activity in the fronto-parietal areas

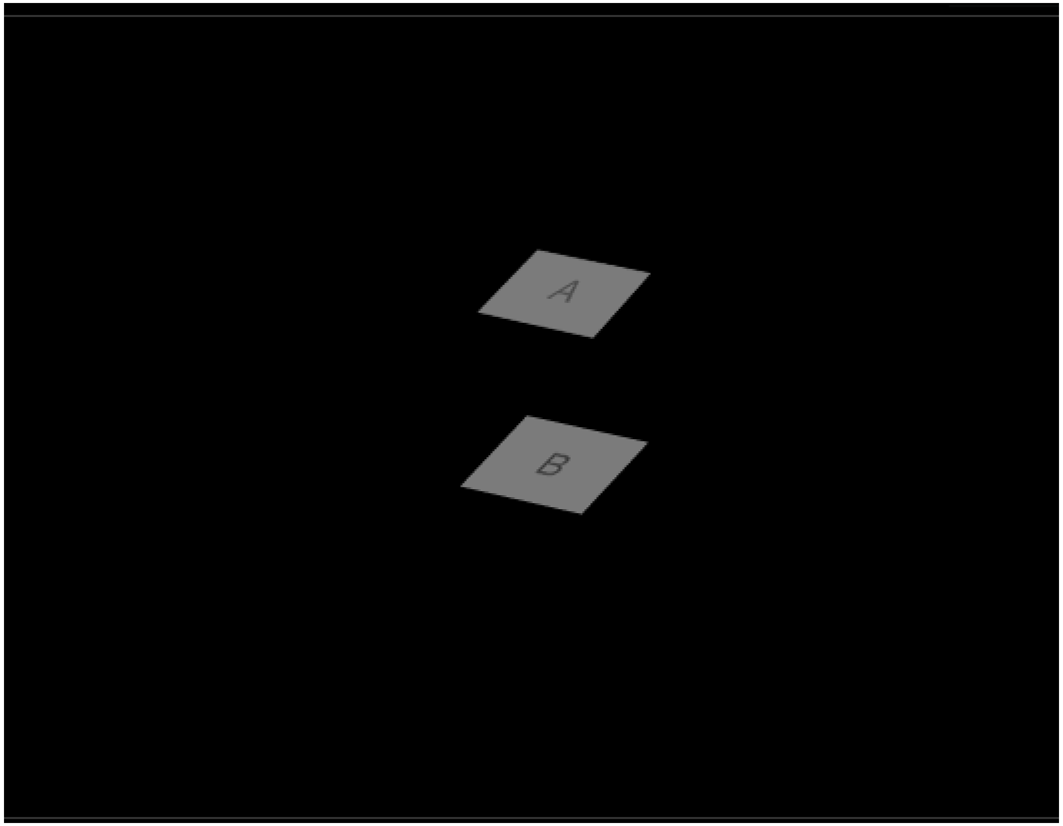
Seeing (visual perception) is the interpretation of the visual input by brain

vs.

- Humans interpret the external world, rather than copying the visual input (as camera does)
- Illusion (mismatch between visual input and percept) is a typical example indicating the interpretation process different from camera
- Illusion can be a crucial clue for understanding the neural mechanisms underlying visual perception

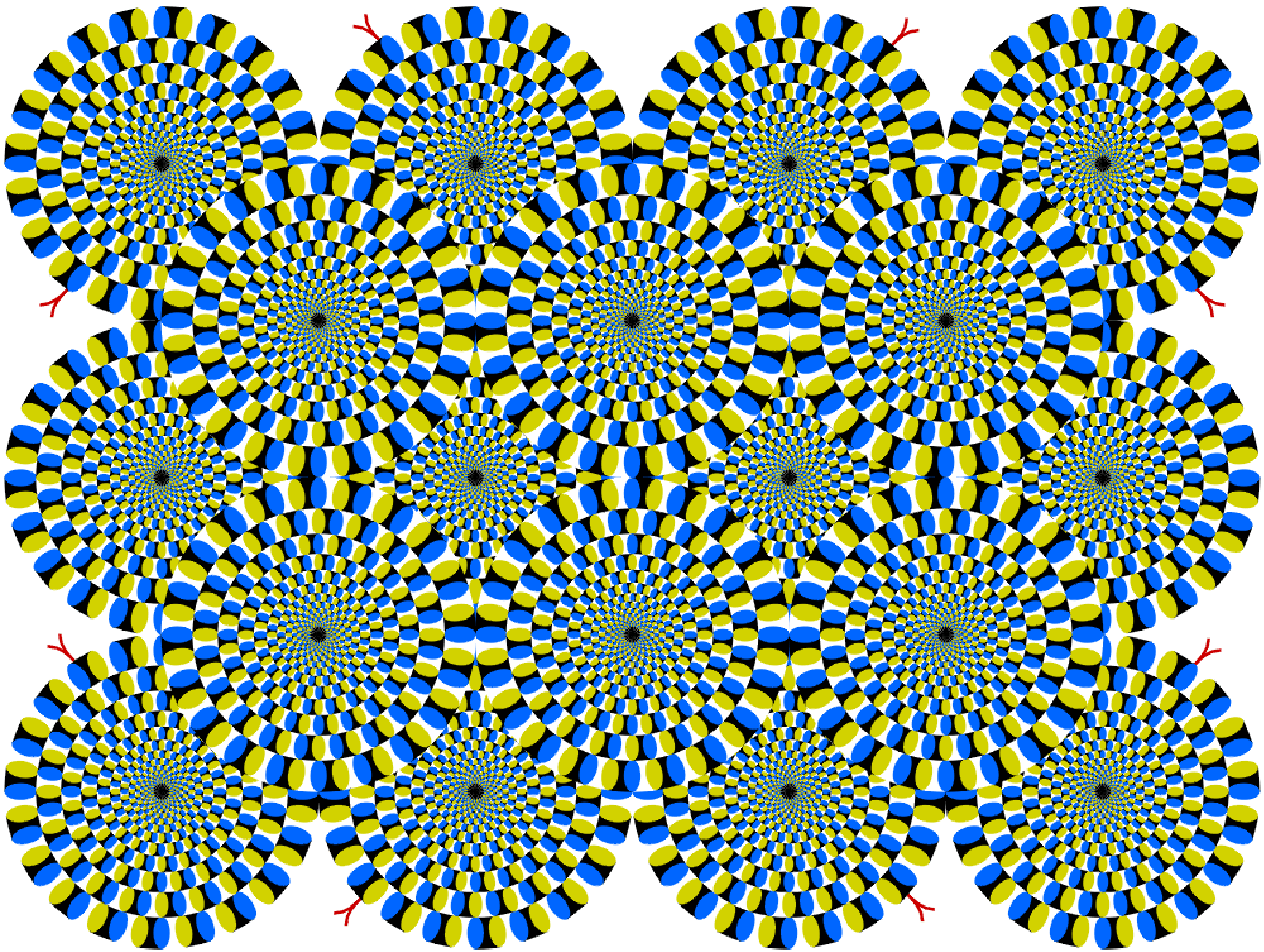
Checkerboard shadow illusion
(Adelson)

"A" looks much darker than "B", but …



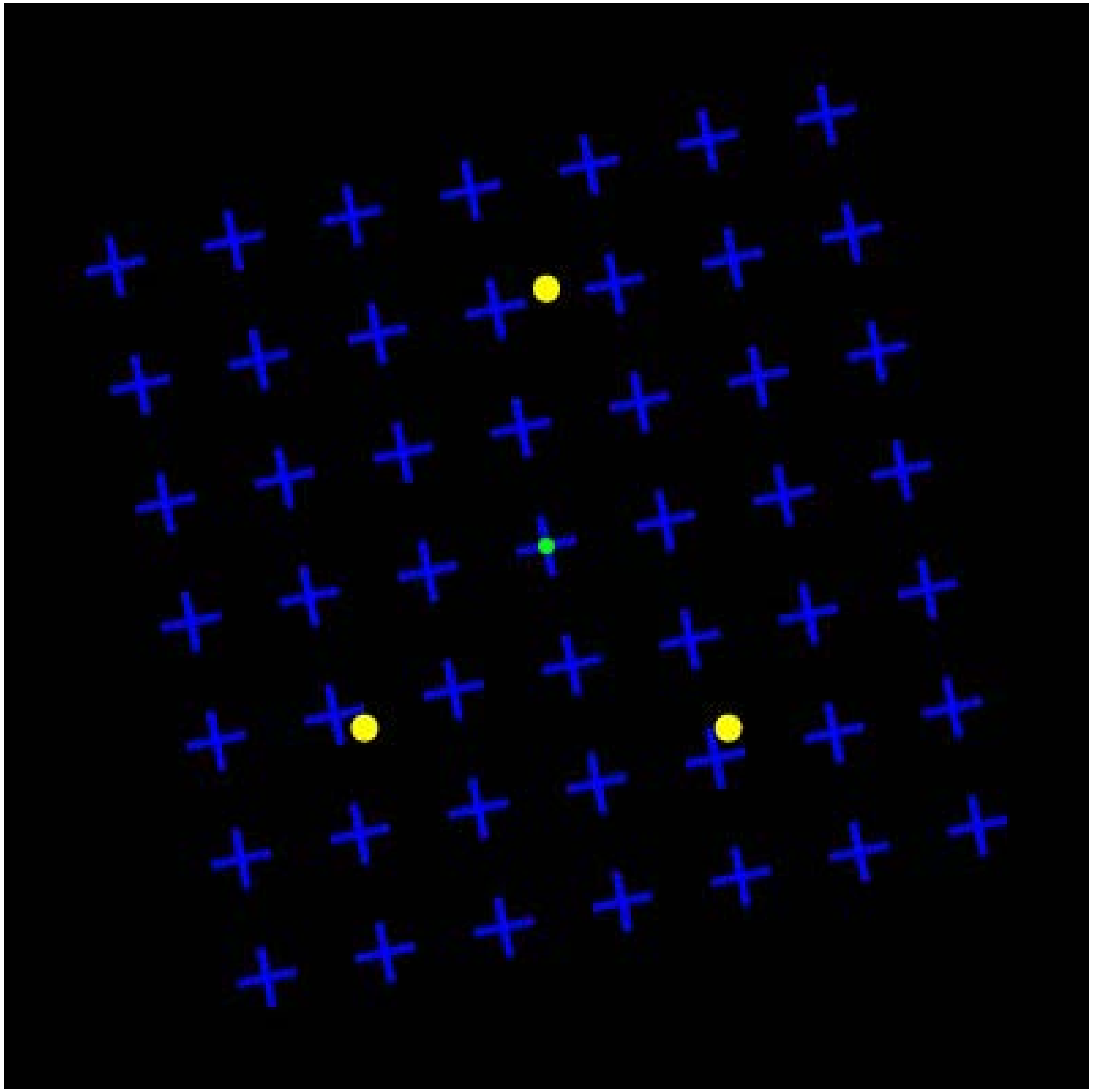
Rotating snake illusion
(Akiyoshi Kitaoka)

Stationary image looks like moving



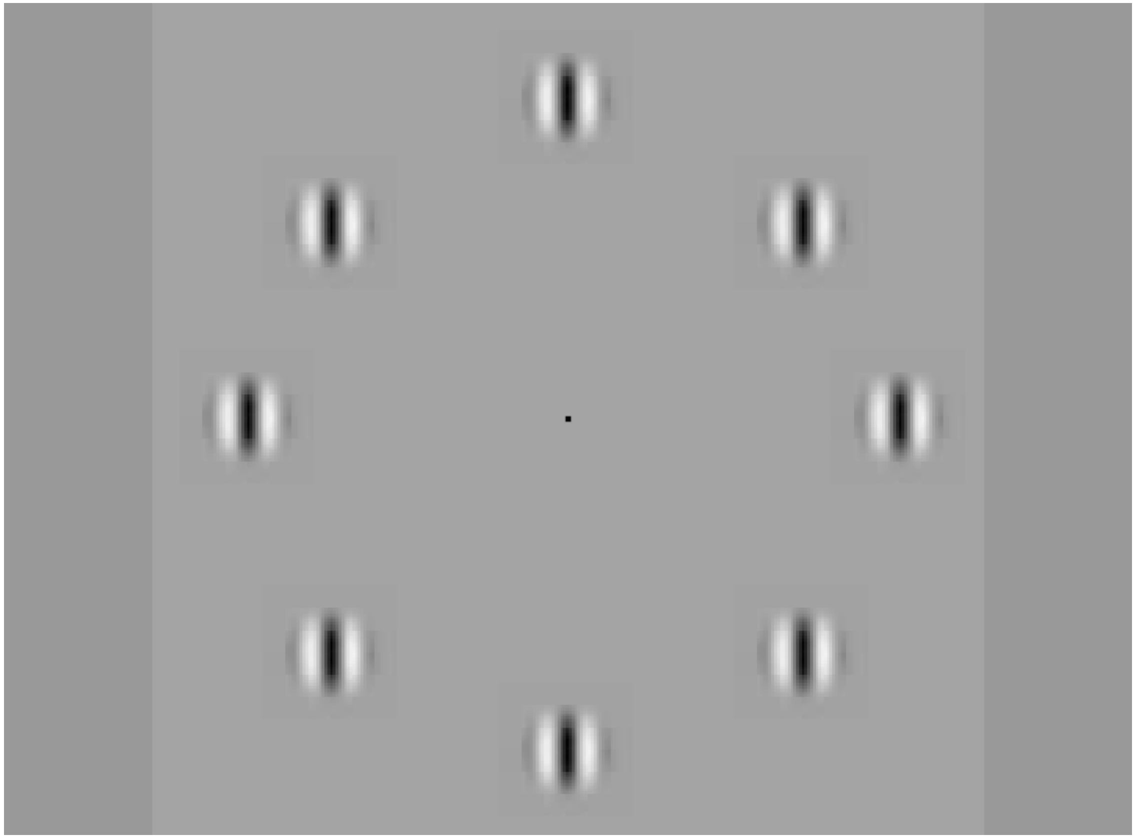
Motion induced blindness
（Bonneh et al.）

Yellow dots disappear and re-appear…



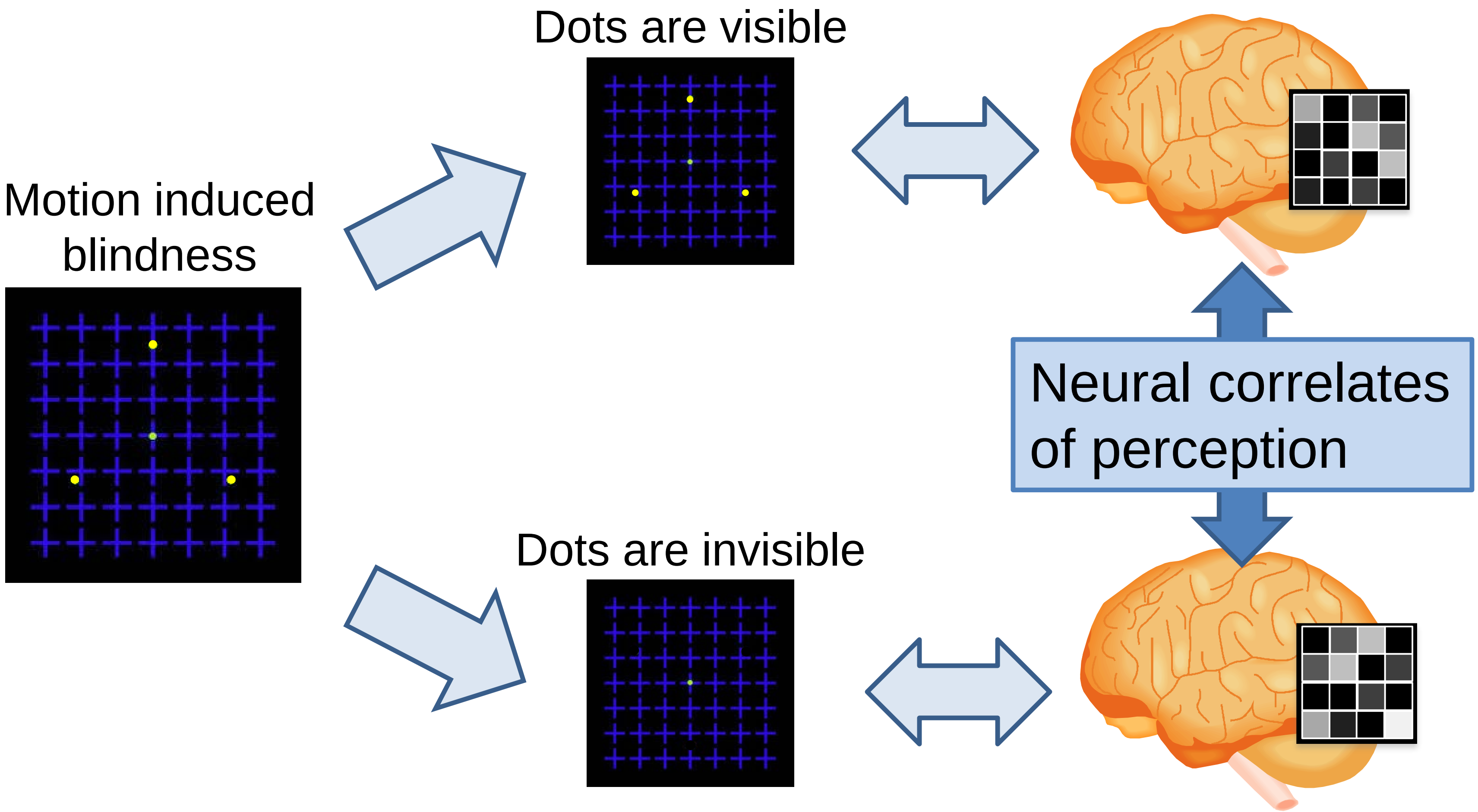
Motoyoshi et al. 2010

Adaptation induced blindness



How to study the neural correlates of perception

Compare the neural activities corresponding to different percepts with keeping the input constant

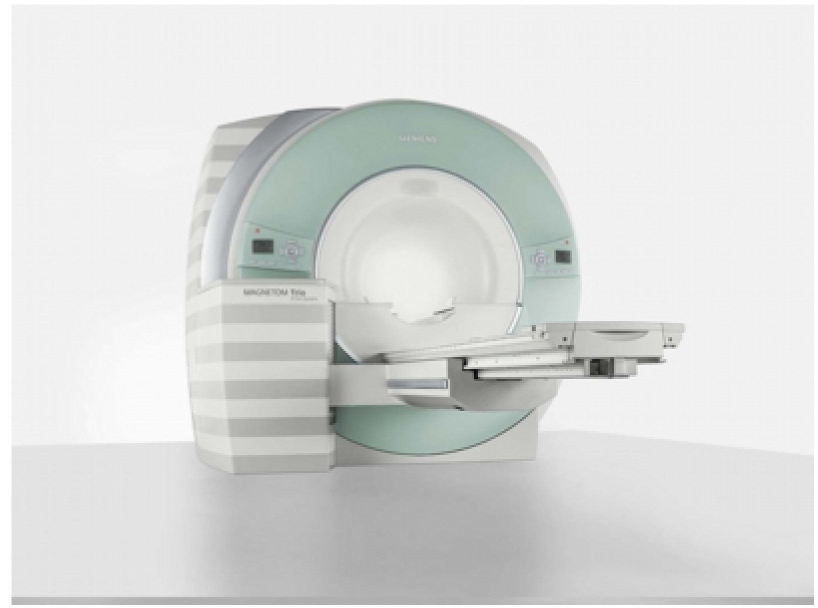


Non-invasive human brain measurement

Magnetoencephalography: MEG

- Electrical activities of neurons
- High temporal resolution (ms)
- Difficult to accurately estimate the locus of activity

Functional magnetic resonance imaging: fMRI



- Changes in blood flow associated with electrical activities of neurons
- Low temporal resolution (s)
- High spatial resolution (mm)

Need to utilize different techniques for each purpose

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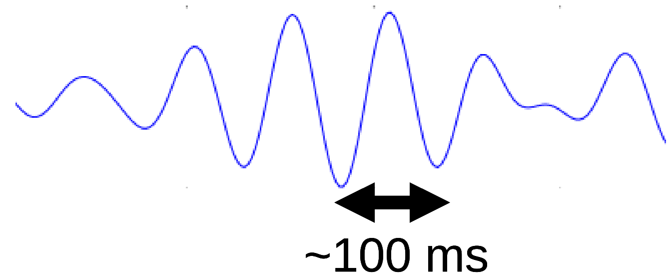
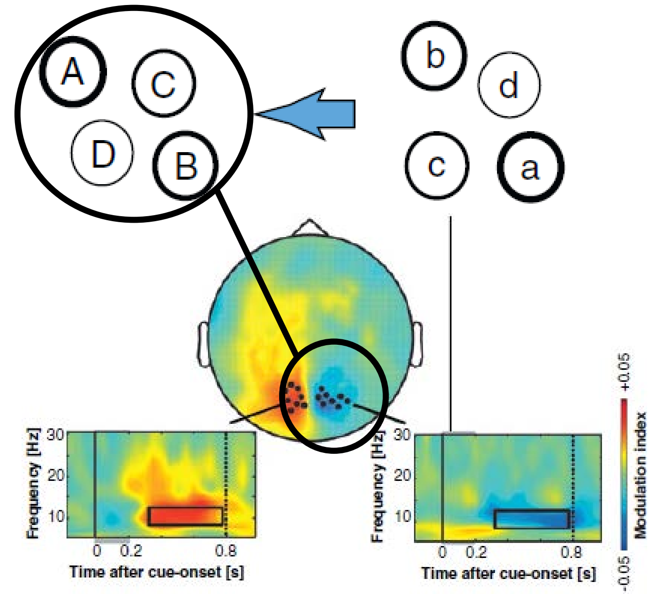
Alpha oscillation



- Neural oscillations at 8-13 Hz
- Increases when you relax
- Originally thought to reflect brain "idling"
- Suppression of irrelevant information?

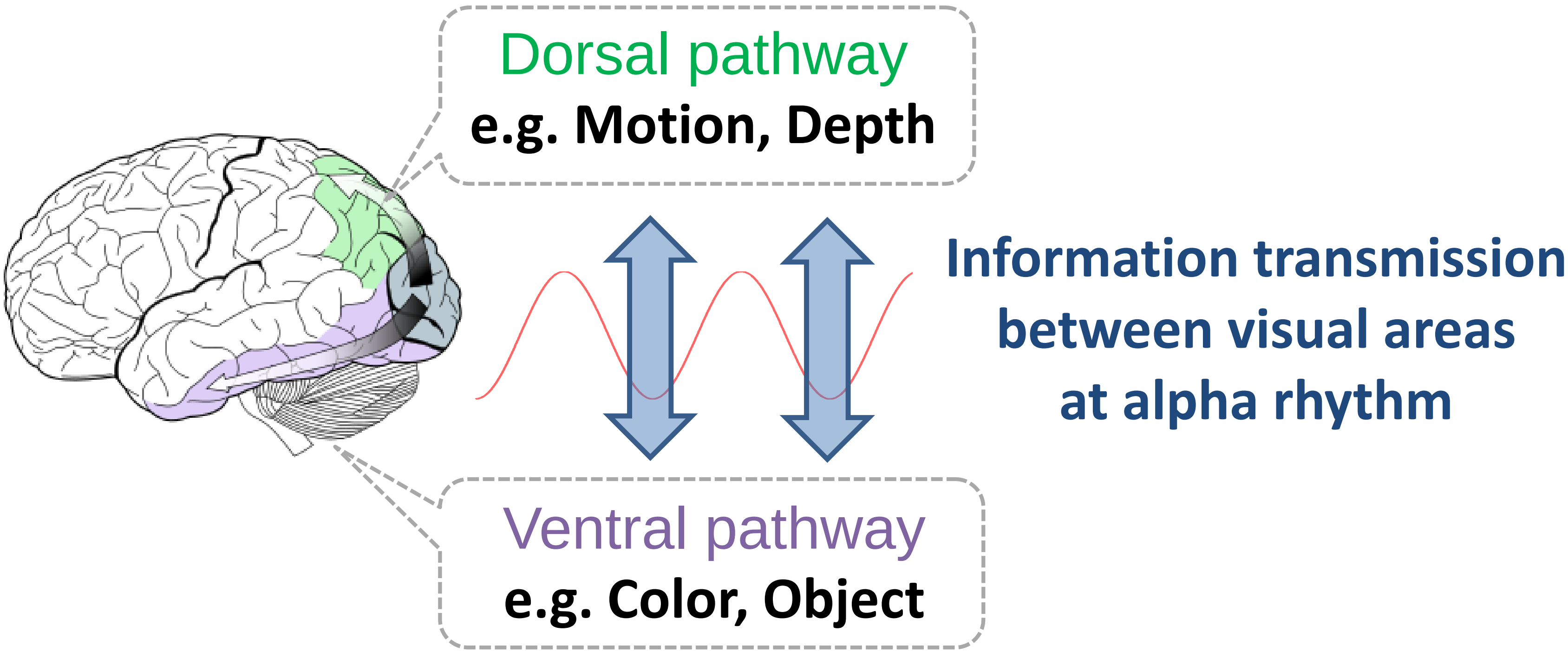
Jensen et al., 2012



Spatial attention suppress contralateral alpha and enhances ipsilateral alpha

What is the functional role of alpha oscillation?

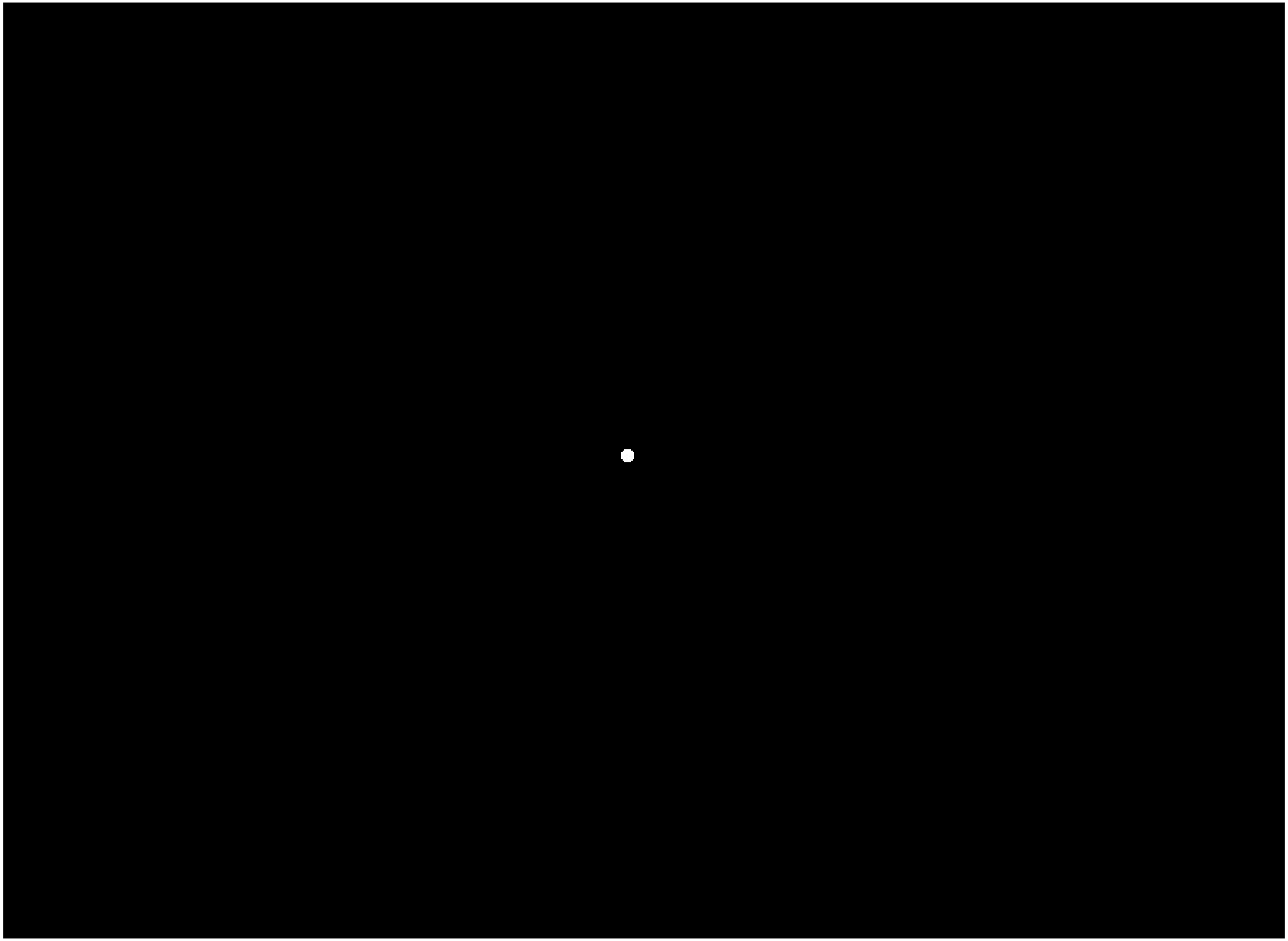
Alpha oscillation as a clock signal for visual processing?



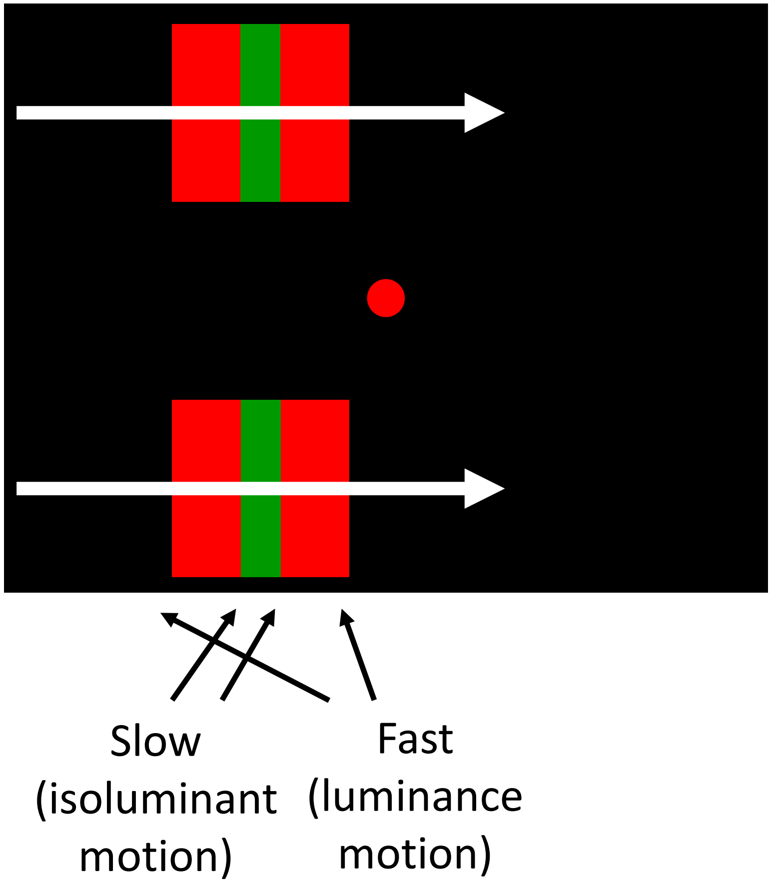
Alpha oscillation might work as a clock signal that determines the timing of interaction between visual areas

Motion-induced spatial conflict

Arnold and Johnston, 2003

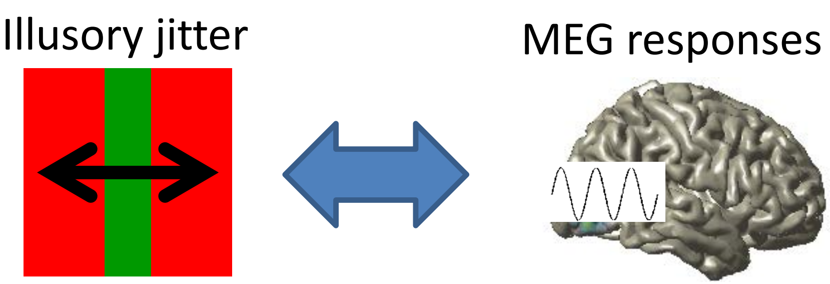


Motion-induced spatial conflict



Arnold & Johnston, 2005

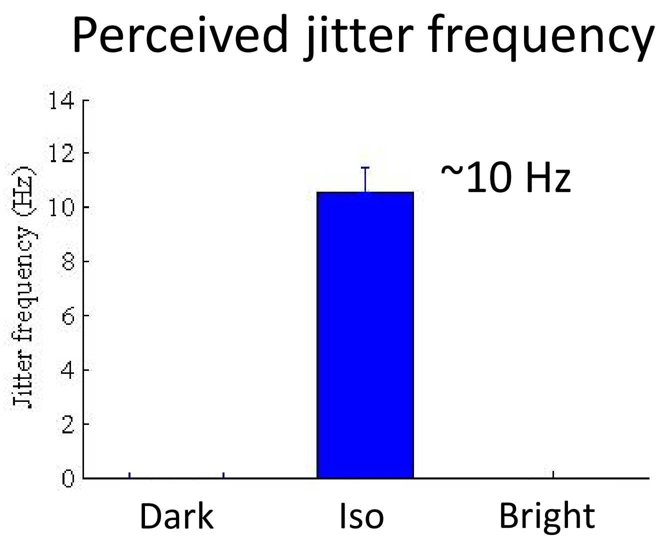
- Red-green borders were set to be isoluminant
- Perceived speed of isoluminant red-green boarders is slower than that of a luminance defined red-black borders
- Isoluminant border is perceived to be jittering

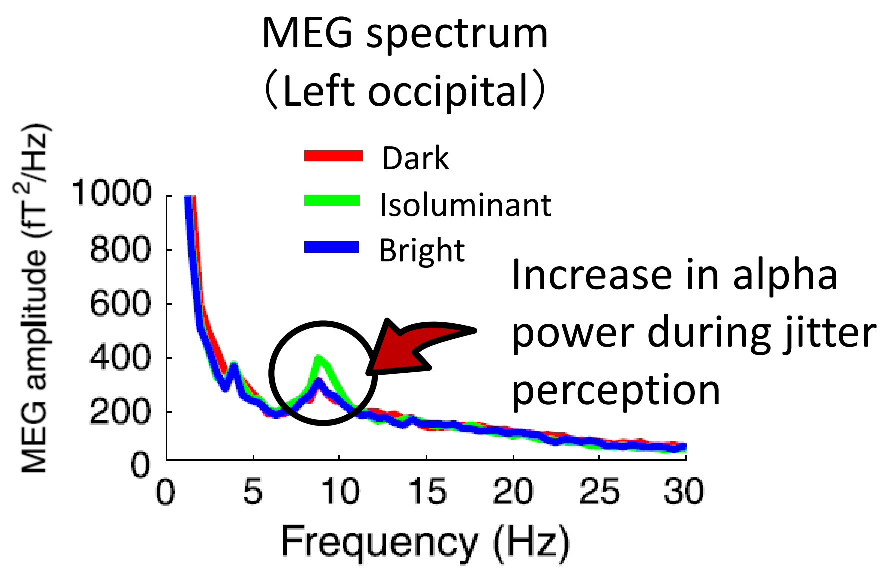


Amano et al., 2008

Green bars were either
(1) darker than, (2) isoluminant with, or (3) brighter than red squares

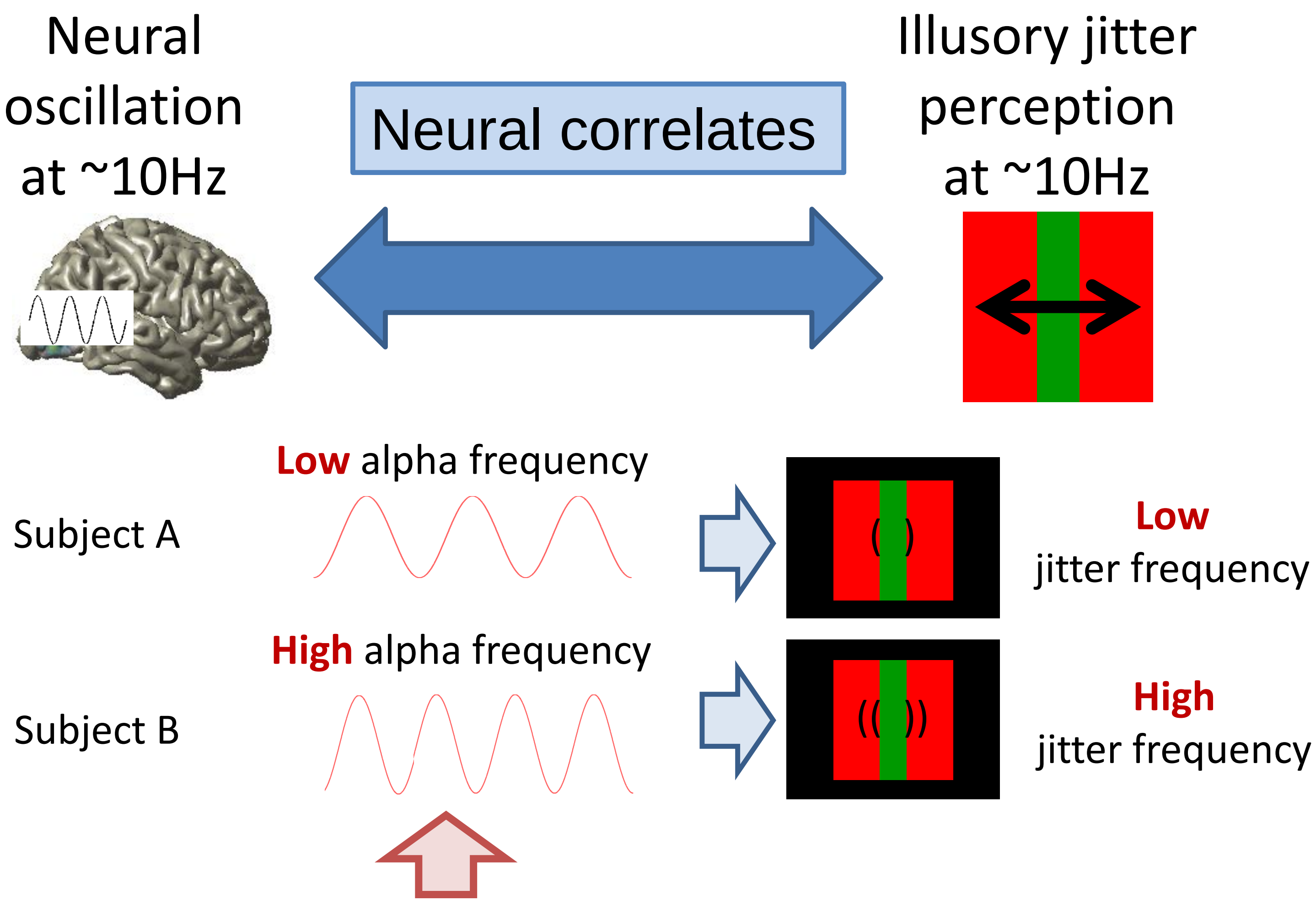
Correlation between jitter perception and alpha oscillation



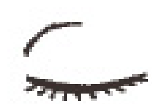


- Frequency of illusory jitter, perceived only in the isoluminant condition, was at around 10 Hz
- Frequency of modulated neural oscillation matches the perceived jitter frequency

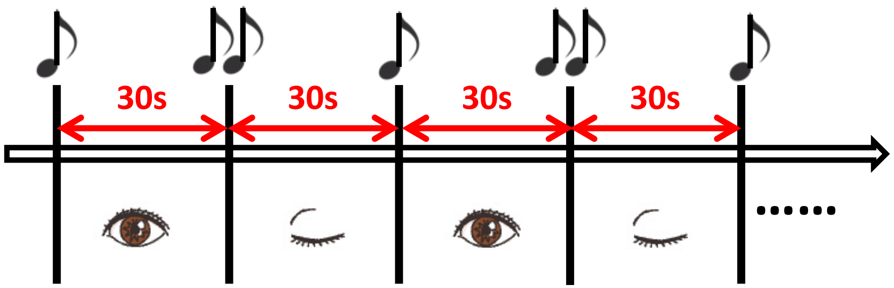
Does perceived jitter frequency reflect individual alpha frequency?



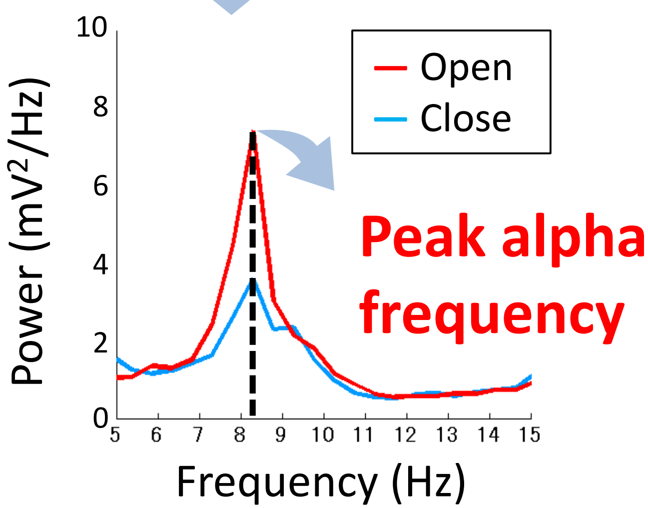
Alpha frequency is measured during rest **BEFORE** jitter frequency measurement



Measurement of alpha oscillation



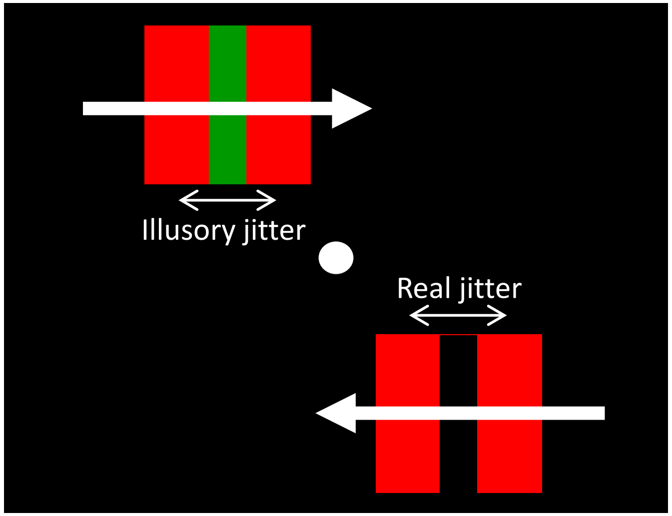
FFT analysis
on MEG data



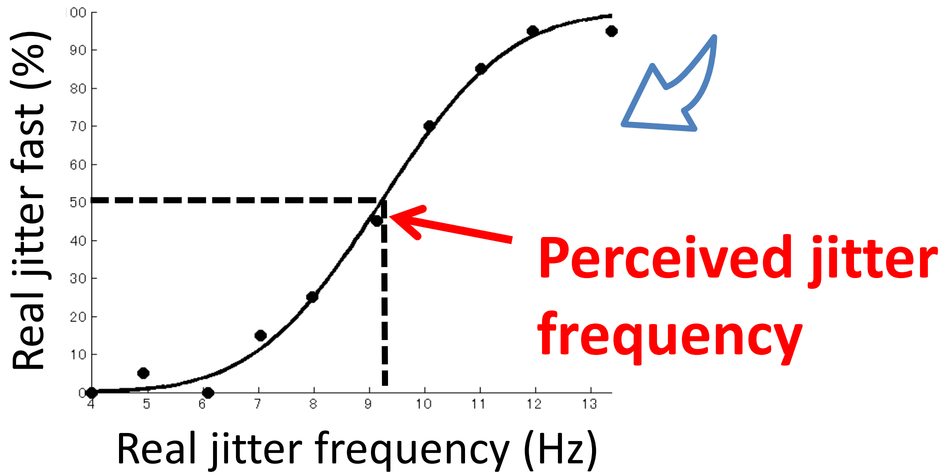
- Open/close eyes
  - One beep: open eyes
  - Two beeps: close eyes
- 5 repetitions of open/close session
- Subjects: 10

- Whole-head MEG system (Elekta)
- Sampling frequency: 500 Hz
- 306 channels

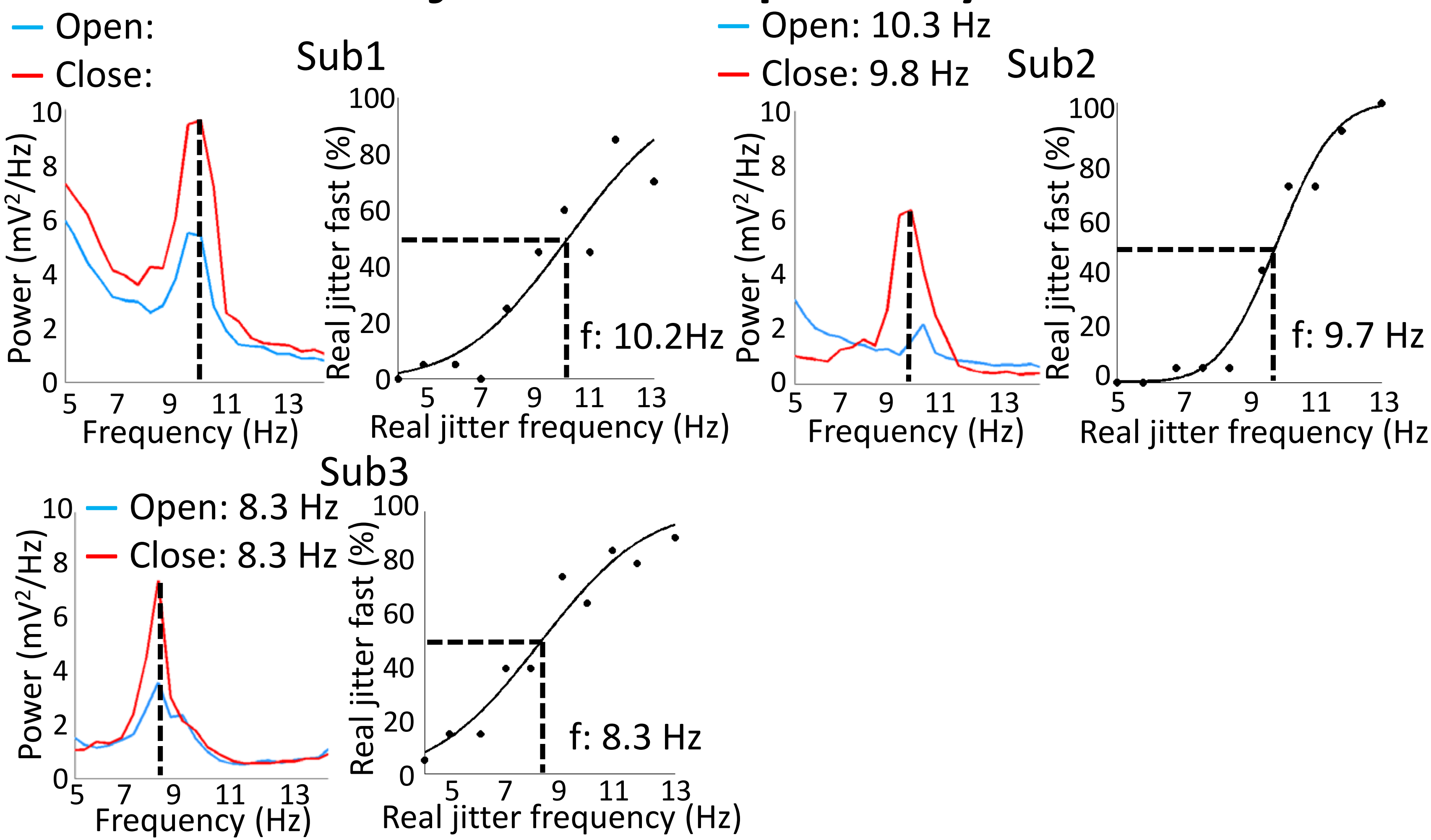
Measurement of perceived jitter frequency



- Frequency of real jitter was randomly chosen from 4-13 Hz (20 times each)
- Subjects judged whether the real jitter is faster than the illusory jitter

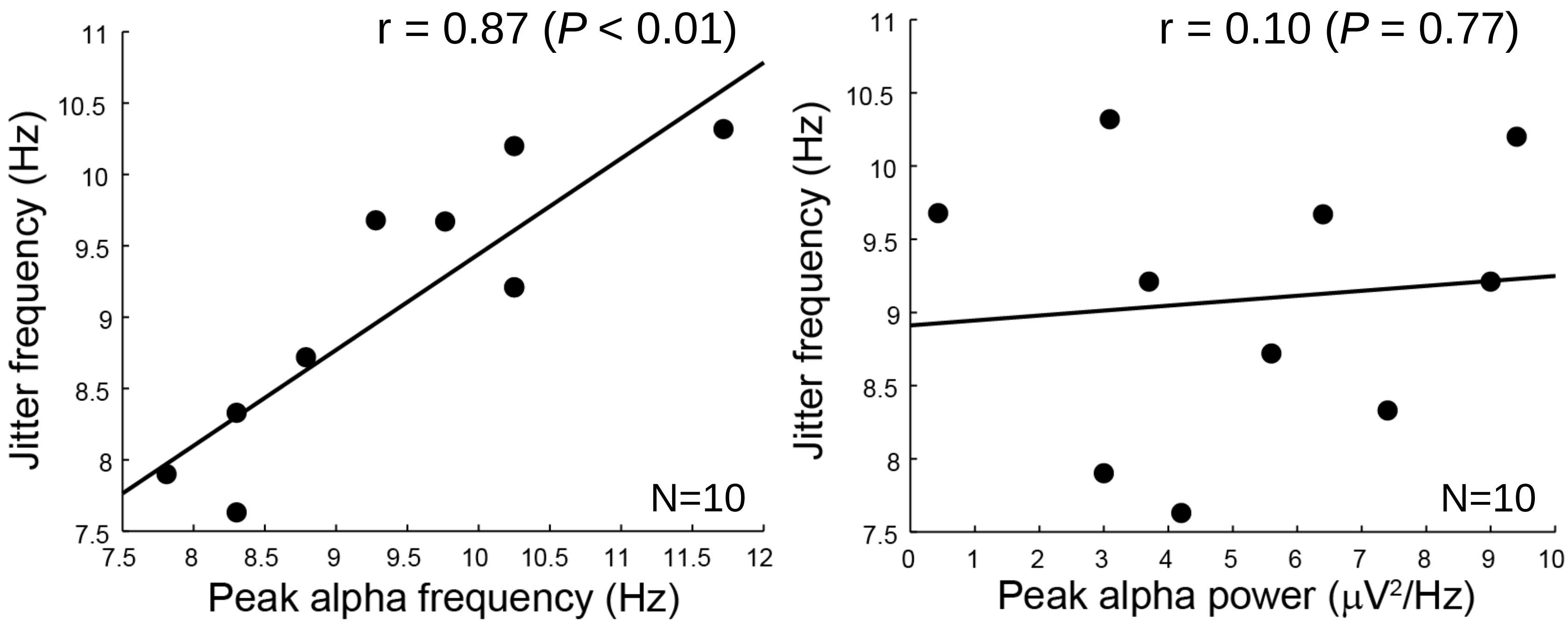


Individual resting alpha and perceived jitter frequency



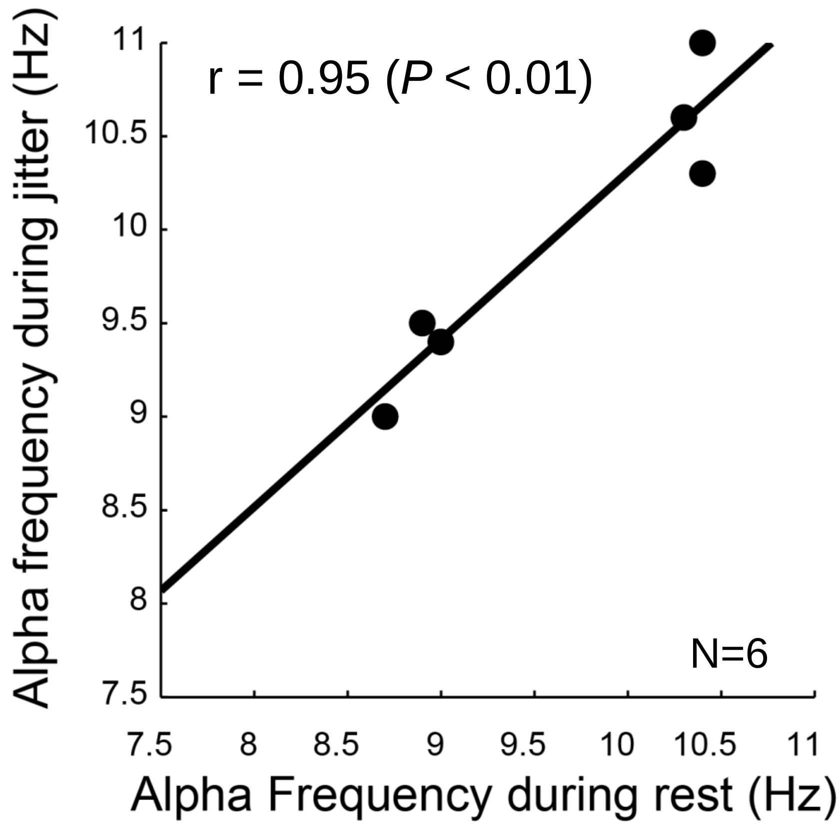
Perceived jitter frequency mirrors individual peak alpha frequency

Individual alpha frequency, not amplitude, correlates with jitter frequency



- Illusory jitter is perceived at the frequency of intrinsic alpha oscillation
- Alpha power is not correlated with jitter frequency

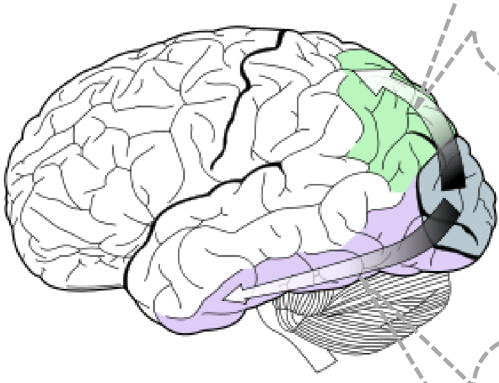
Resting state alpha frequency is kept constant during jitter perception



Peak alpha frequency during the perception of illusory jitter was highly correlated with that during the resting state

Possible functional role of alpha oscillation

Dorsal pathway



Ventral pathway

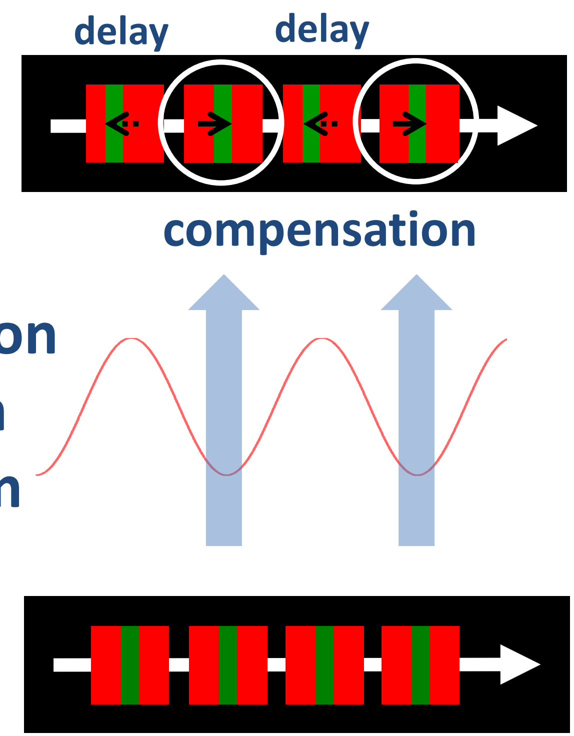
Motion-based position representation

High temporal resolution
Low spatial resolution

Object-based position representation

Low temporal resolution
High spatial resolution

Update of position representation at alpha rhythm



Alpha oscillation may function as a clock signal for the interaction between visual areas

Summary

- Alpha oscillation is enhanced when illusory jitter is perceived
- Perceived jitter frequency was highly correlated with the peak alpha frequency during the resting state
- Alpha oscillation is the neural correlates of illusory jitter perception

Alpha oscillation might work as a clock signal that determines the timing of interaction between ventral and dorsal visual areas

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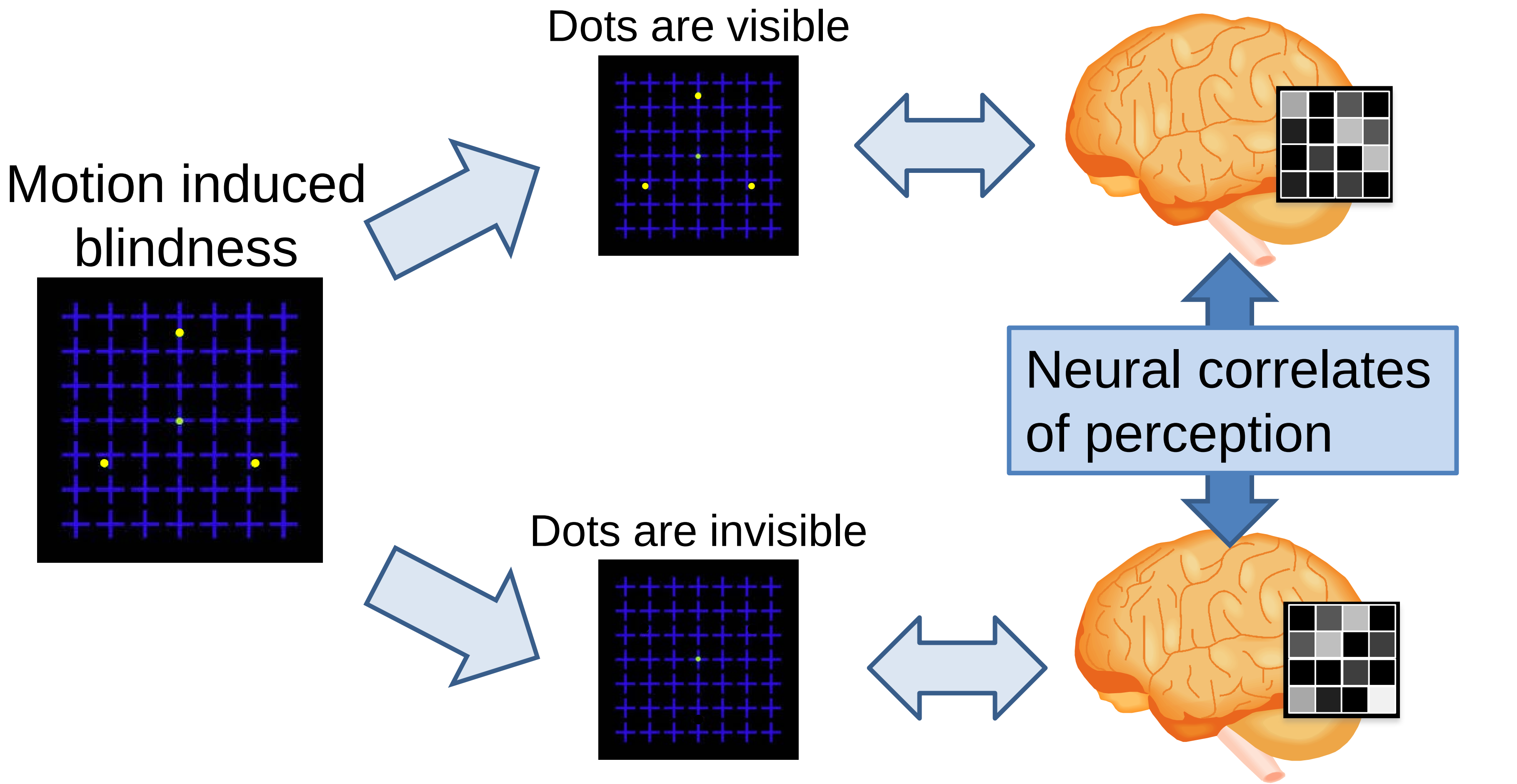
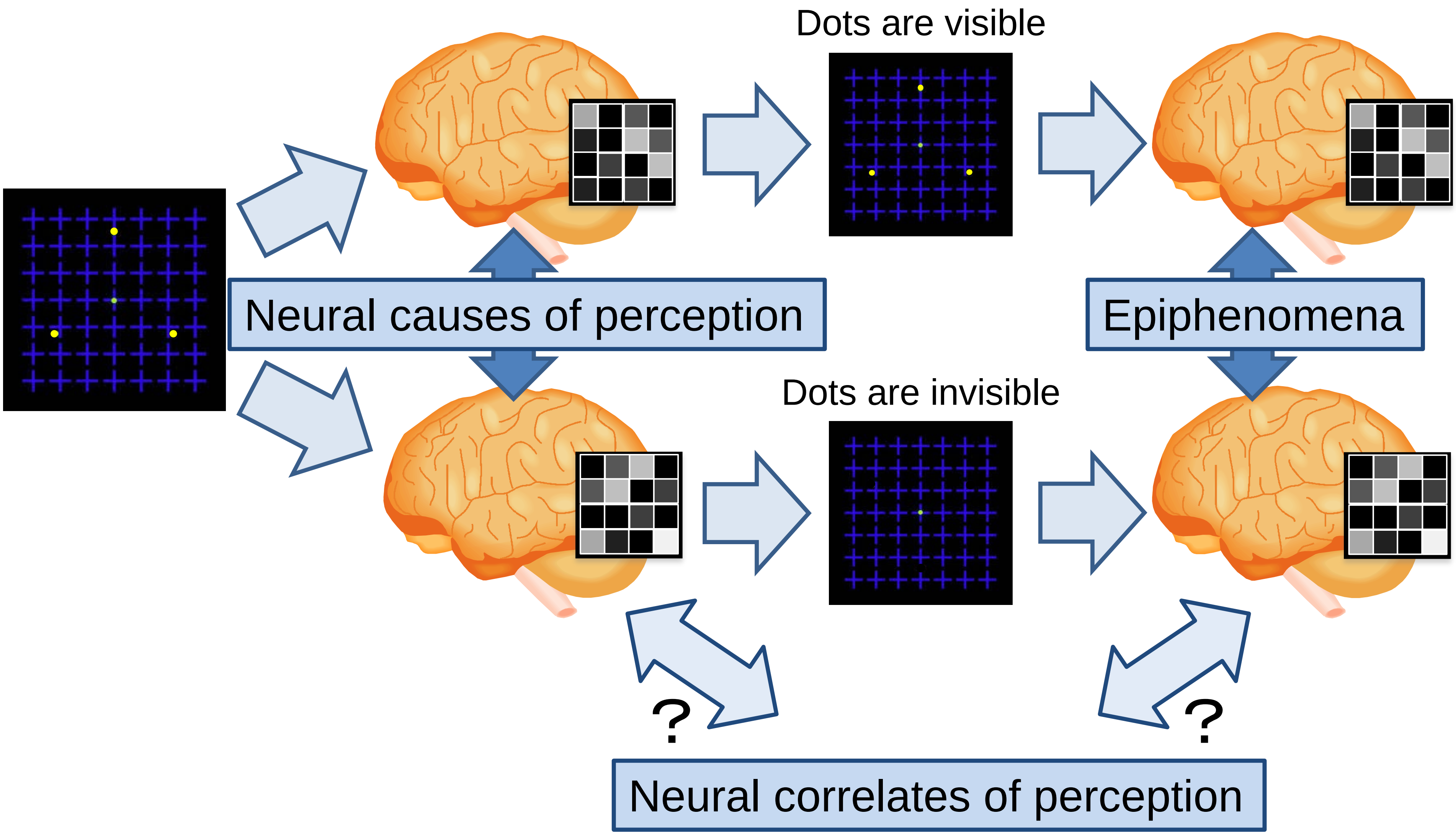
How to study the neural correlates of perception

Compare the neural activities corresponding to different percepts with keeping the input constant

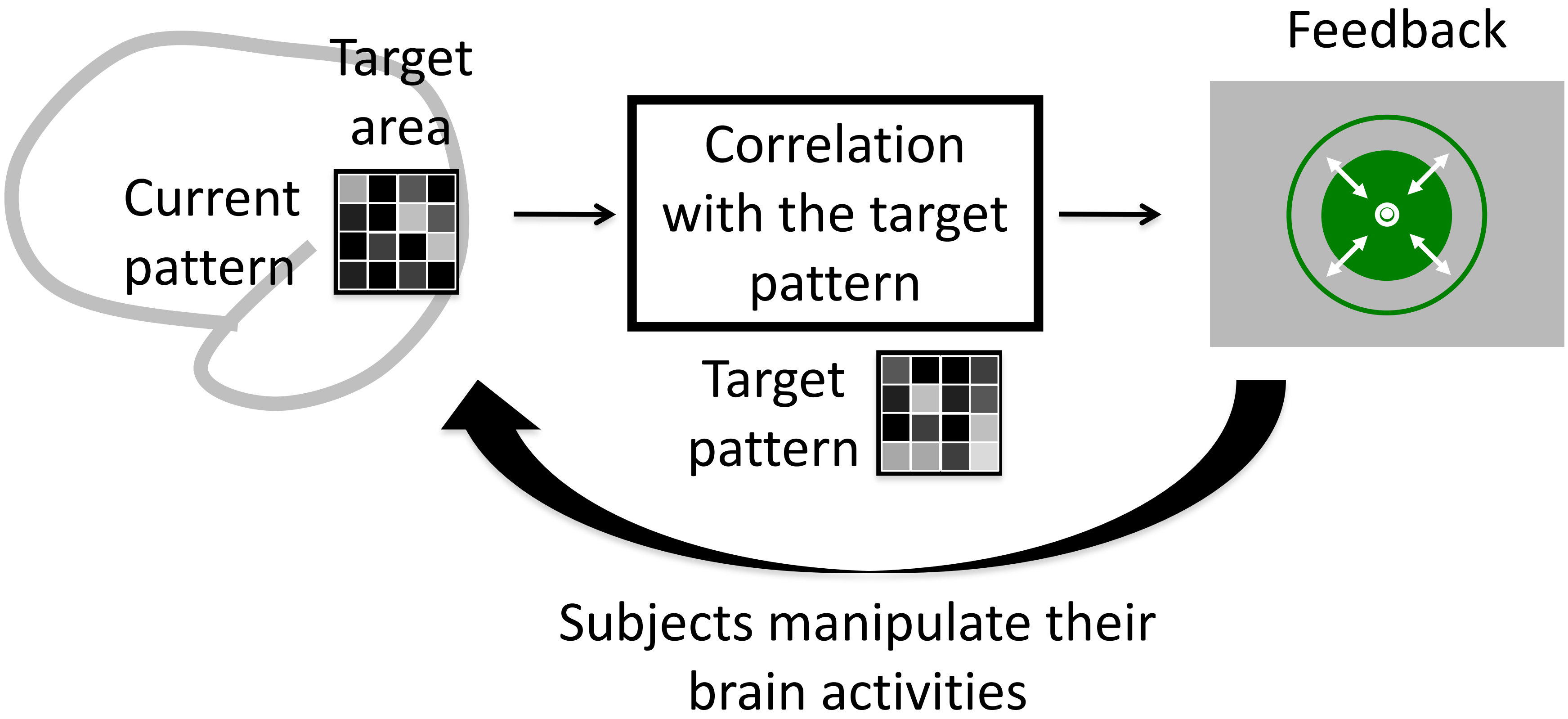


Neural correlates are not necessarily neural causes of visual perception



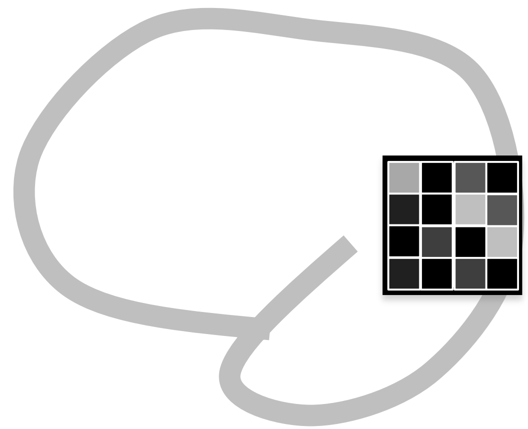
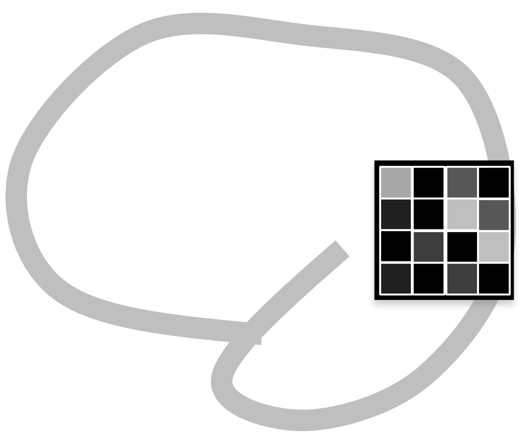
FMRI decoded neurofeedback (DecNef)

Shibata et al., 2011



A specific brain activity pattern in a specific area can be induced with DecNef

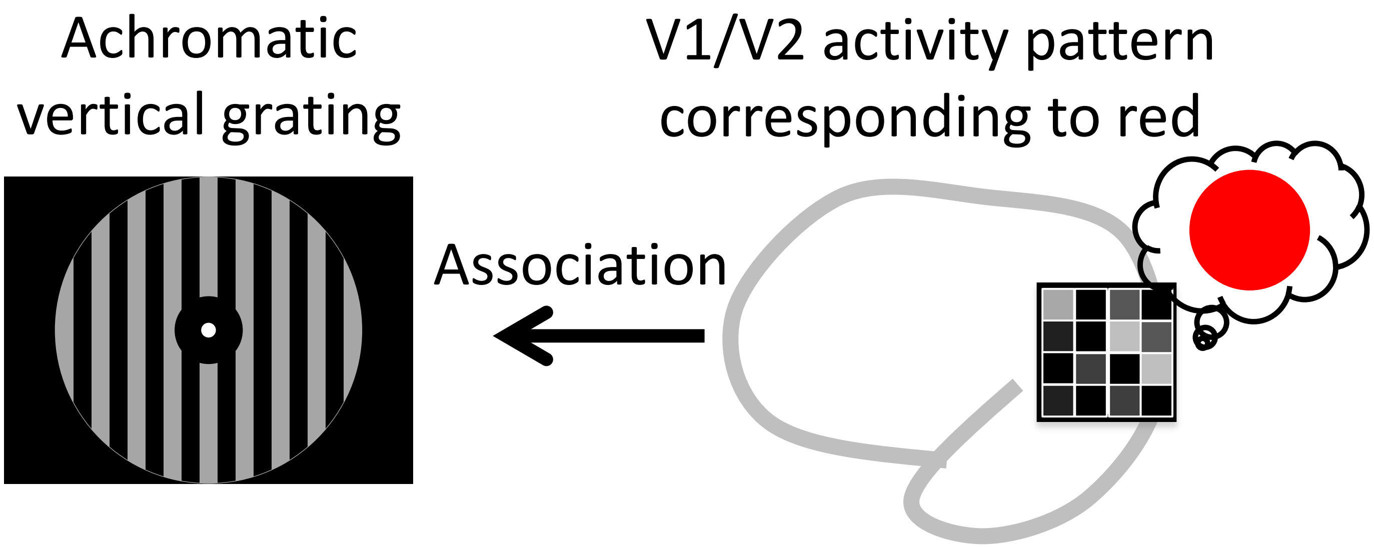
Decoded neurofeedback (DecNef) as a tool for cognitive neuroscience

	Variable		Observation
Correlation analysis	**Perception** **Behavior** **Cognition**	⟷	
DecNef		→	**Perception** **Behavior** **Cognition**

Shibata et al., 2011

Purpose

Create color perception associated with an orientation by manipulating neural activity in the primary and secondary visual areas (V1/V2) using decoded fMRI neurofeedback



Is an achromatic grating perceived to be reddish?

Experimental procedure

- Day 1: Retinotopic mapping
- Day 2: Color decoder construction

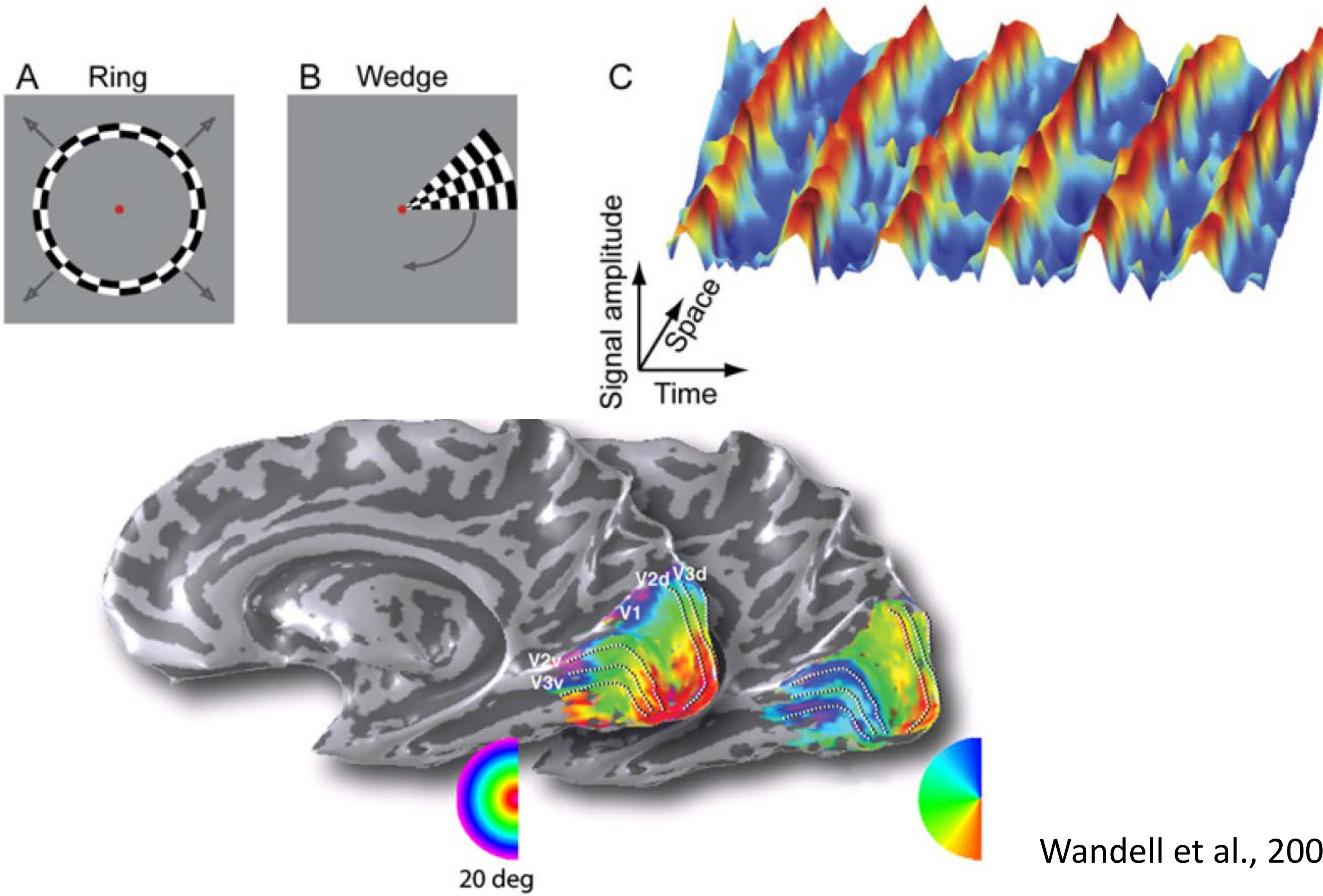
  1–2 weeks

- Day 3: Decoded neurofeedback training
- Day 4: Decoded neurofeedback training
- Day 5: Decoded neurofeedback training
  Subjective color test
  Chromatic psychometric function measurement

- **12 subjects** participated in the 5-day session
- **6 control subjects** participated in only a subjective color test and chromatic psychometric function measurement

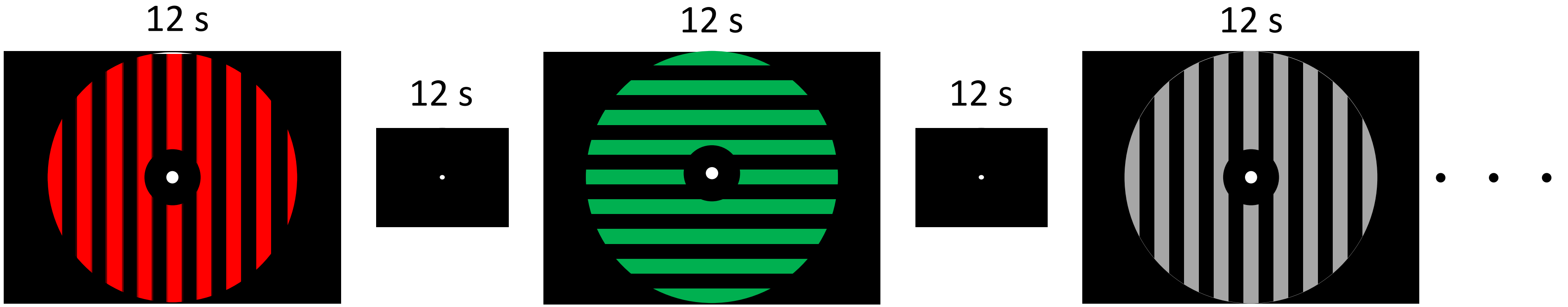
None of the subjects were colorblind

Day 1: Retinotopic mapping

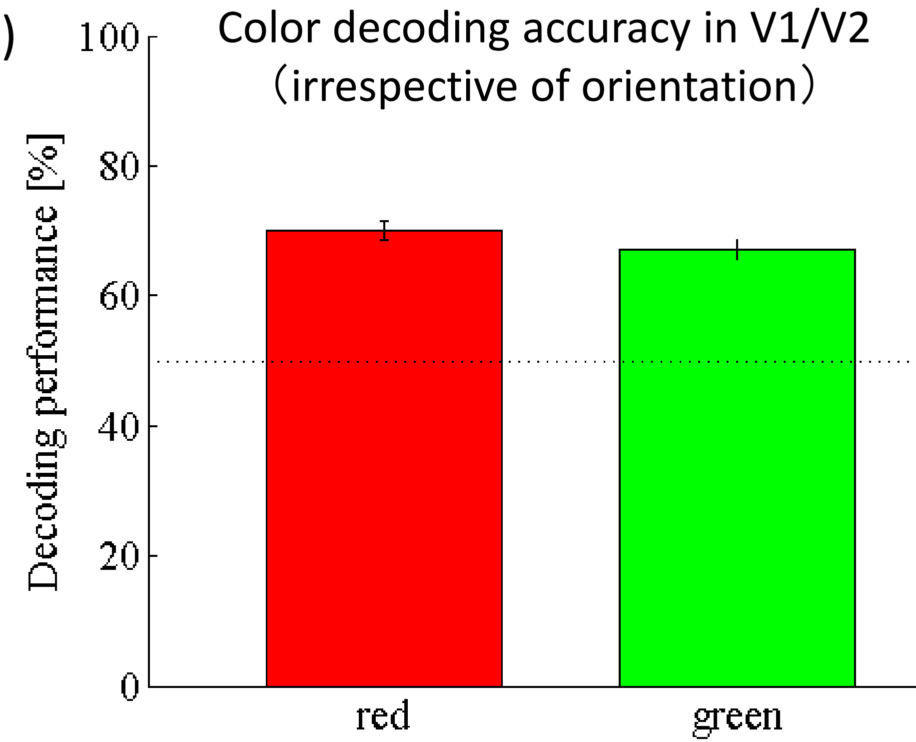


Wandell et al., 2007

Day 2: Color (red vs. green) decoder construction

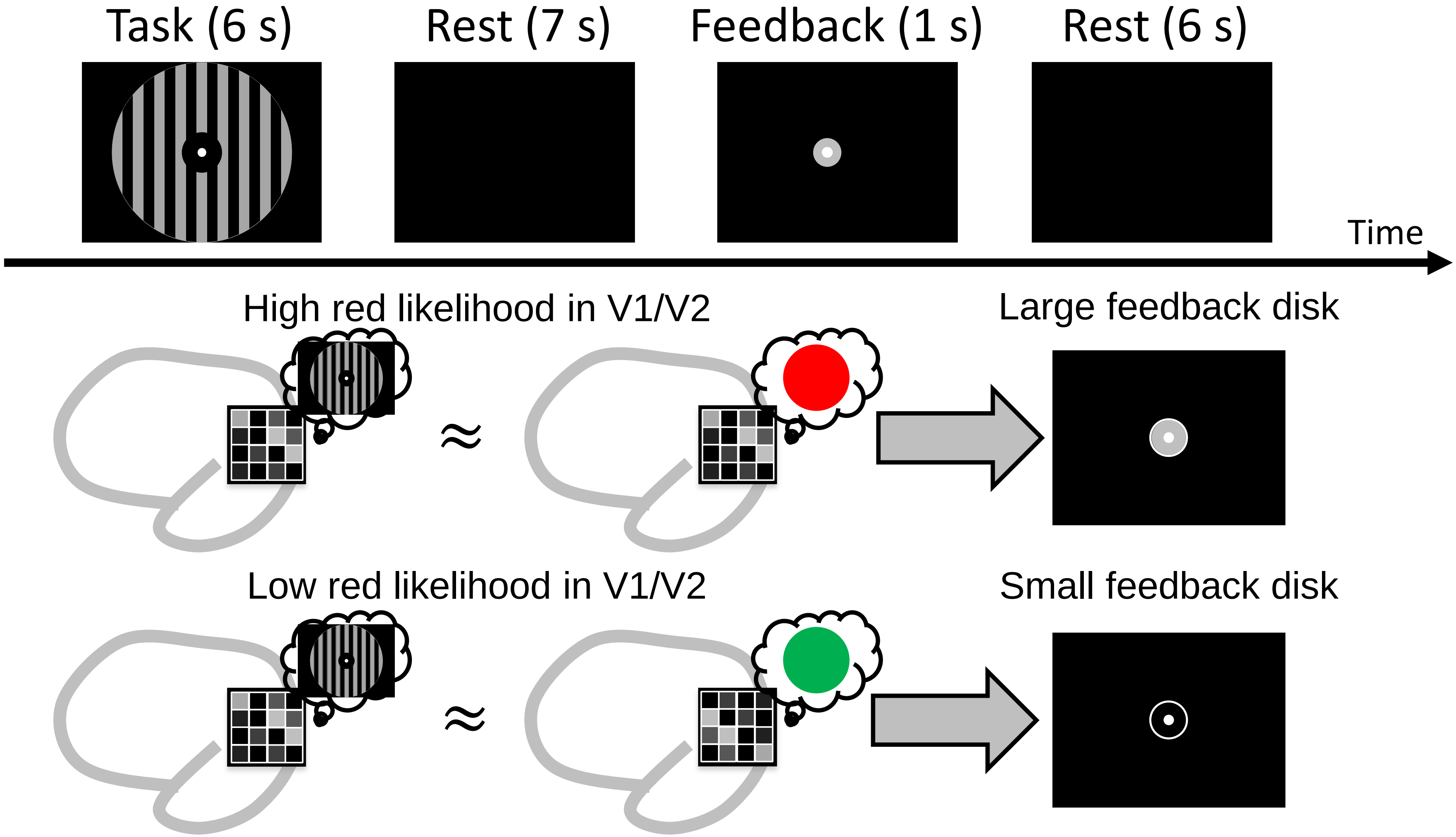


- Each combination of color (red/green/gray) and orientation (vertical/horizontal) was randomly presented 24 times in 12 runs
- Green and gray are set to be perceptually equiluminant to red
- SF: 1 cycle/deg, TF: 0.5 Hz



Red likelihood of V1/V2 activity pattern was calculated by sparse logistic regression (SLR) (>0.5, red; <0.5, green)

Days 3-5: Decoded neurofeedback training



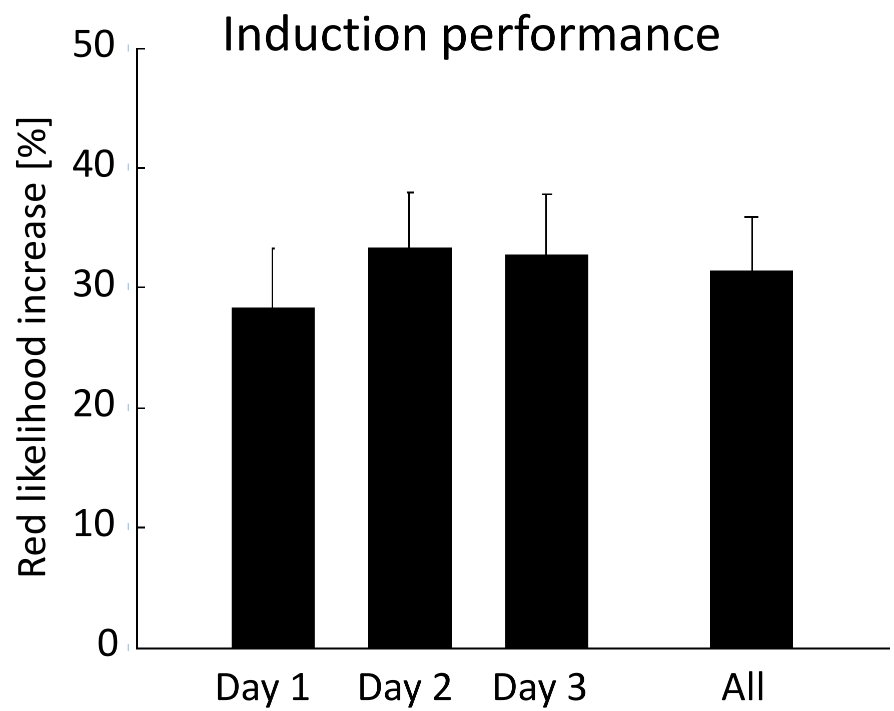
Task: “Somehow regulate your brain activity to make the feedback disk as large as possible”

V1/V2 activity pattern during the presentation of achromatic vertical grating became "reddish"

The strategy of induction

- "I did mental multiplication."
- "I tried to remember scenes of TV programs or video games. I also imagined watching music videos."
- "I counted numbers."
- "I imagined singing or running. I also calculated or remembered sentences."
- "I tried to remember what I did yesterday."
- … and so on.

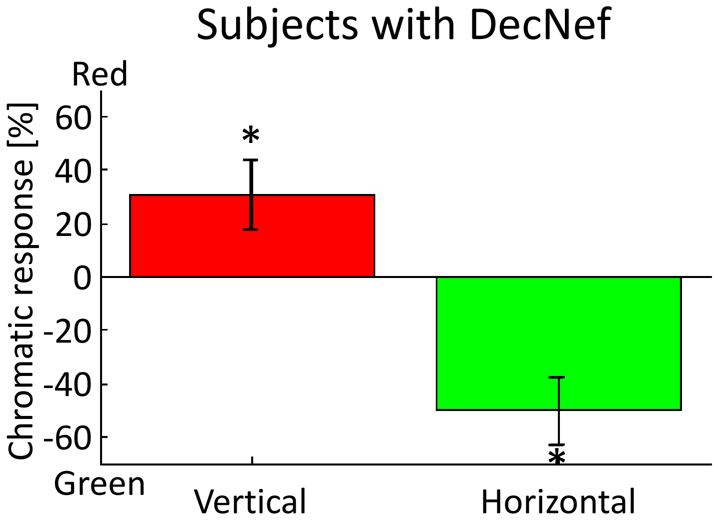
None of these reported strategies was related in any way to the target color (red)



relative to the likelihood of an achromatic vertical grating being classified as the target color (red) in the decoder construction stage

Day 5: Subjective color test

- Each achromatic grating was presented 10 times
- Duration, 1.5 s; ISI, 4.5 s
- Judge the color of the inner grating (red, green or achromatic)

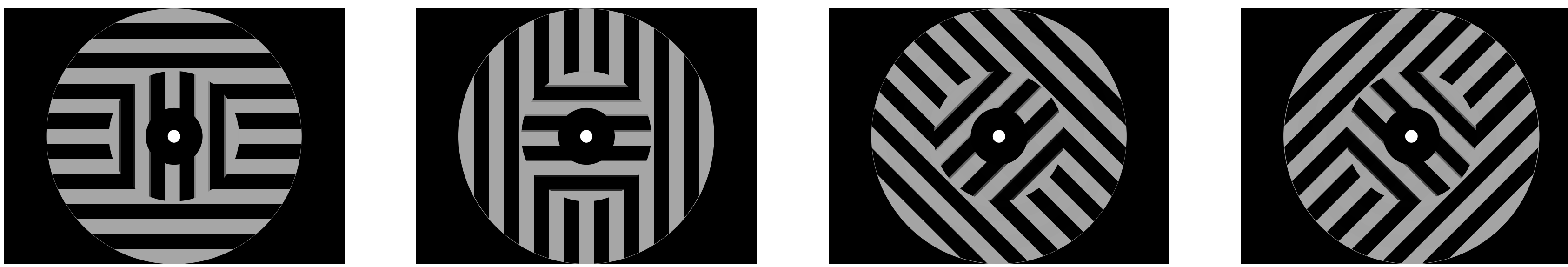


Vertical grating used for DecNef was perceived to be reddish

Day 5: Chromatic psychometric function measurement

- 32 stimuli (4 orientations × 8 colors) were randomly presented
  - Orientation

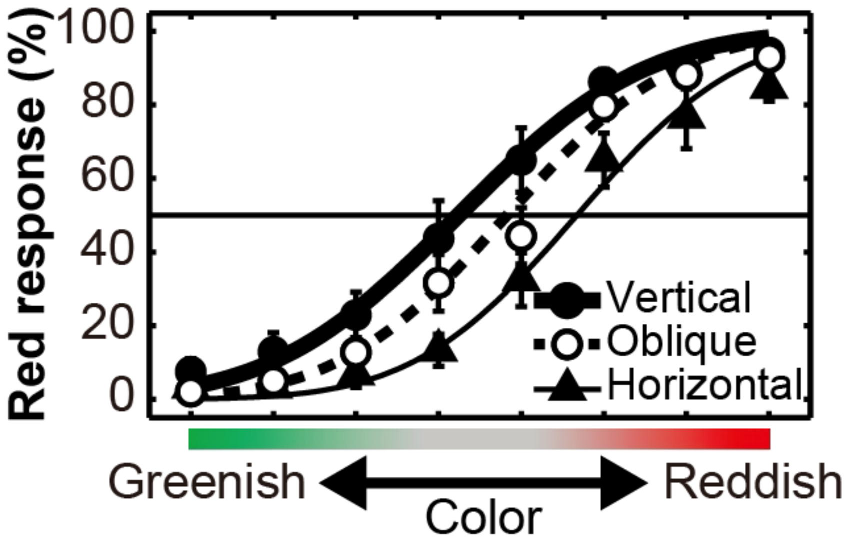
Vertical Horizontal +45 deg -45 deg



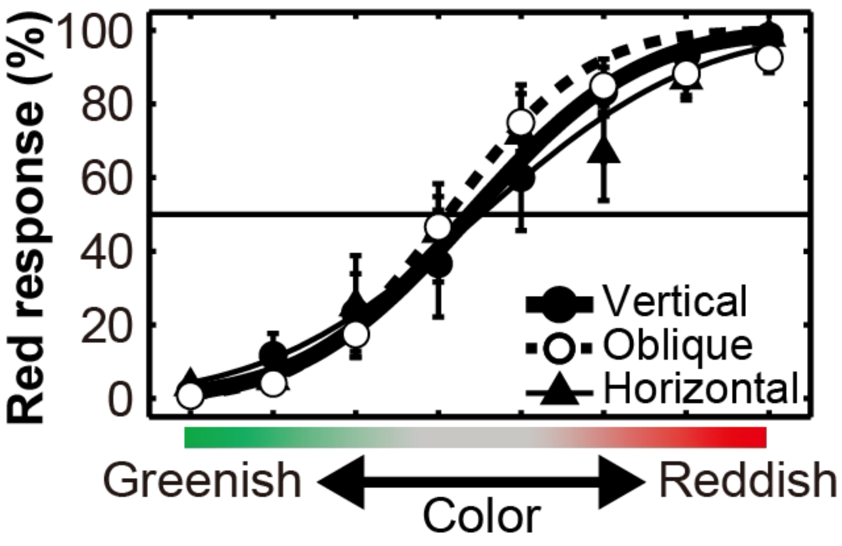
  - Color
    - Inner: 8 levels from greenish to reddish (middle is gray)
    - Outer: gray
- Judge the color of the inner grating (red vs. green)

Shift in psychometric function by DecNef training

Subjects with DecNef

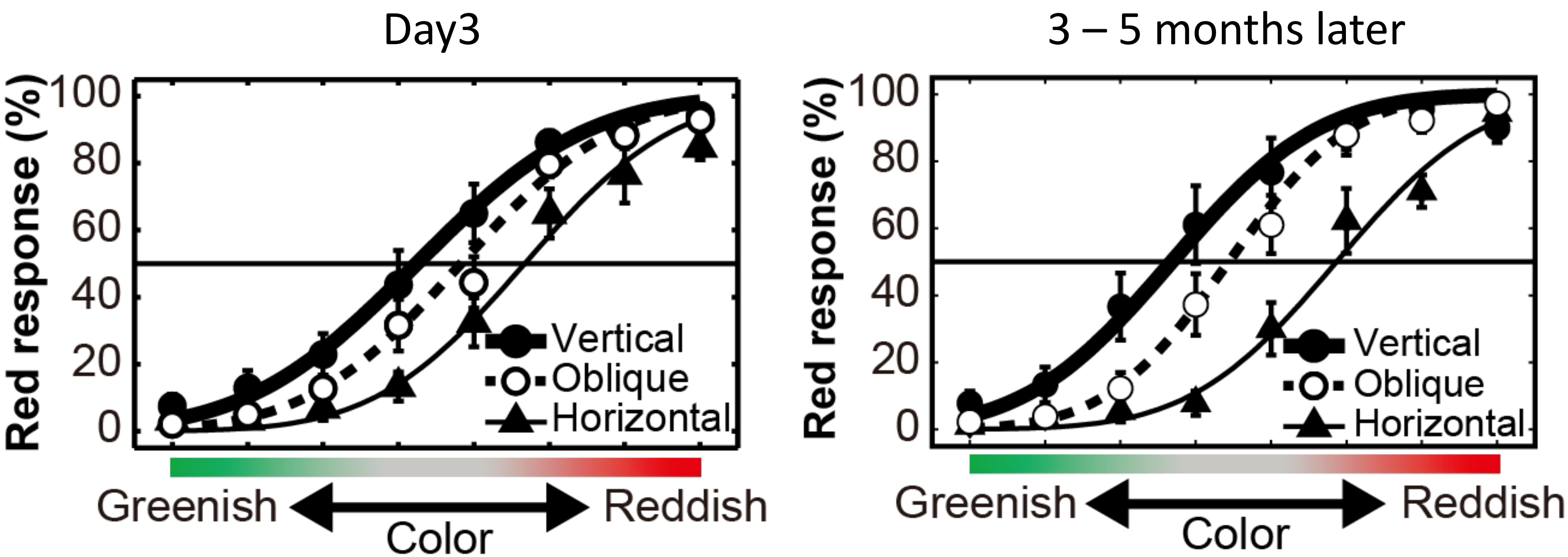


Control subjects



Orientation-specific change in color perception by DecNef

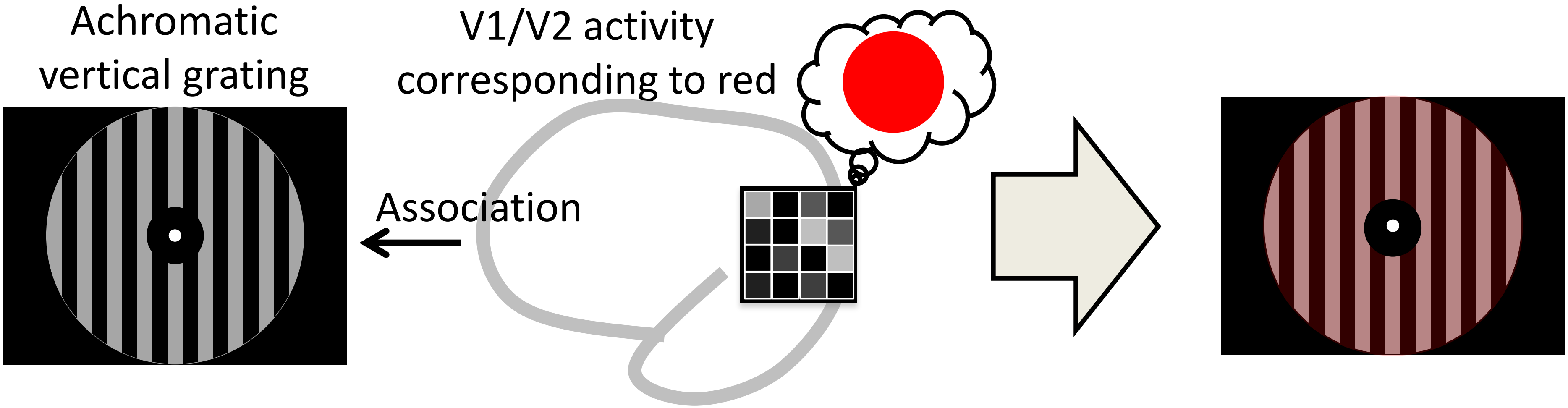
Long-lasting effect of DecNef training



Color perception associated with an orientation is long-lasting, as has been reported for other types of associative learning

Summary

Using decoded fMRI neurofeedback, we created long-lasting color perception associated with a specific orientation



The early visual cortex has the capability of creating an orientation-specific color perception

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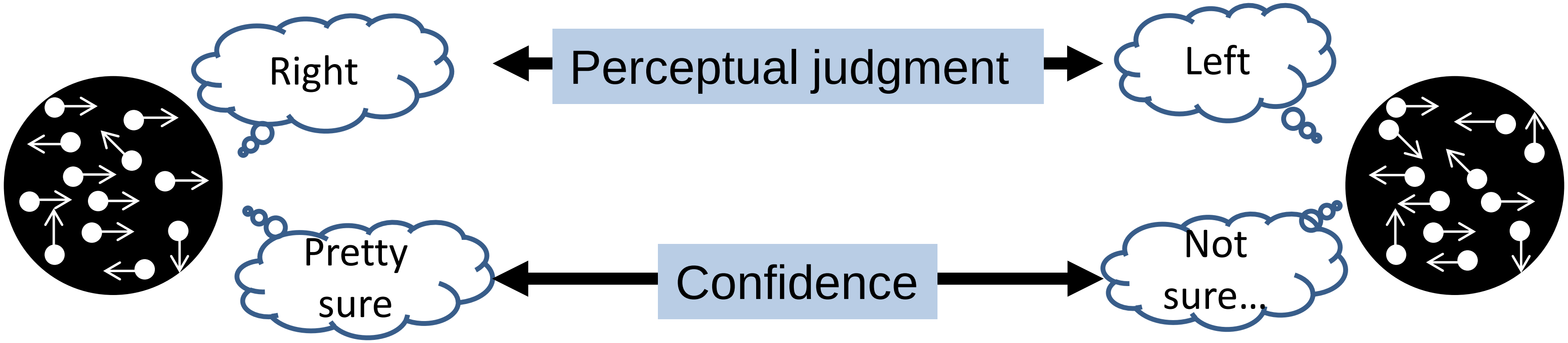
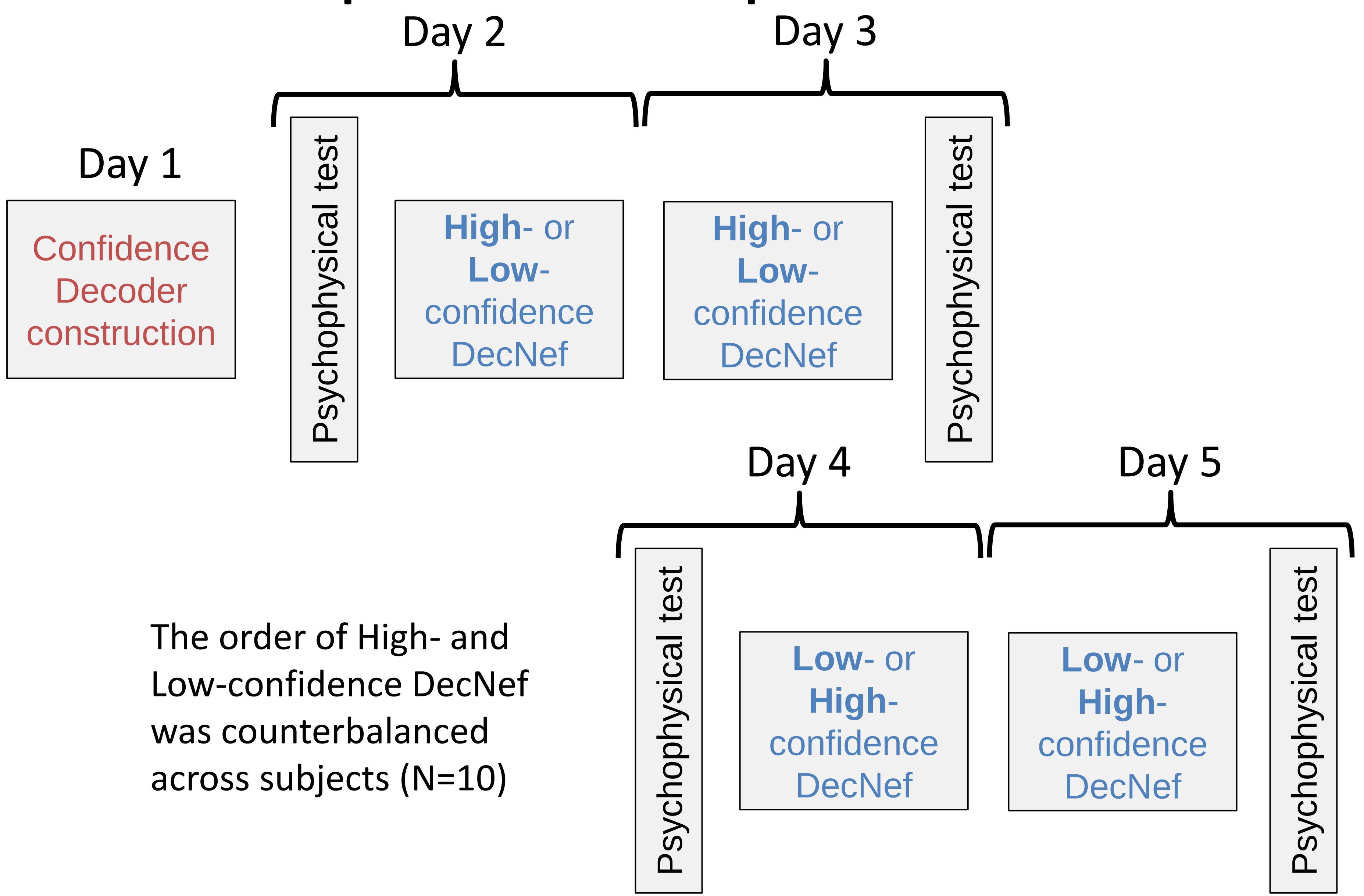
Confidence in perceptual judgment



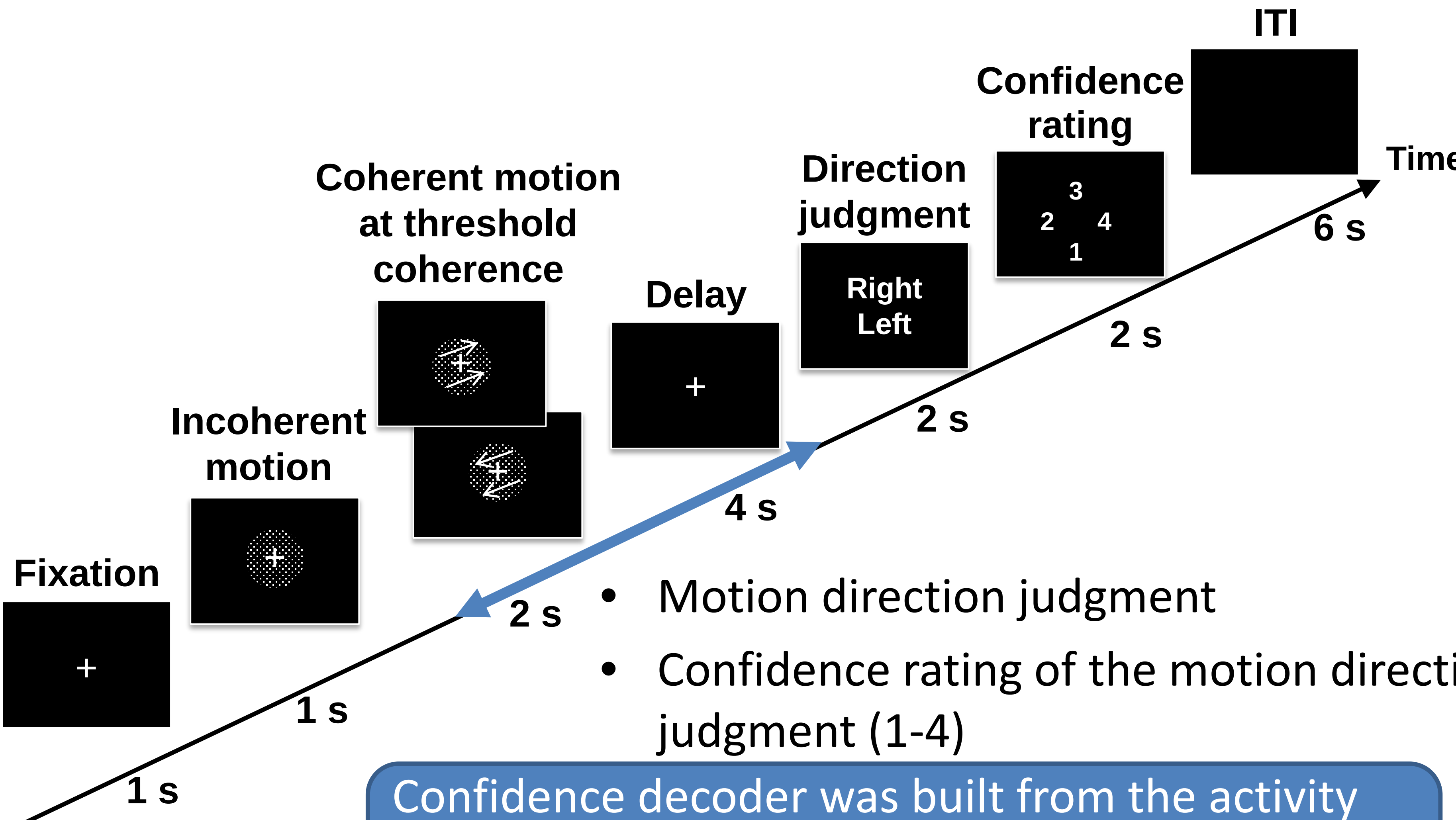
- Confidence is a meta-cognitive function for decisions
- Confidence generally reflects perceptual accuracy but can dissociate from accuracy (e.g. blidsight)
- Confidence affects a variety of cognitive functions
- LIP, DLPFC, and Pulvinar are associated with confidence (e.g. Kiani et al. 2009, Komura et al. 2013)

Are these areas causally associated with the confidence of perceptual judgment?

Experimental procedure



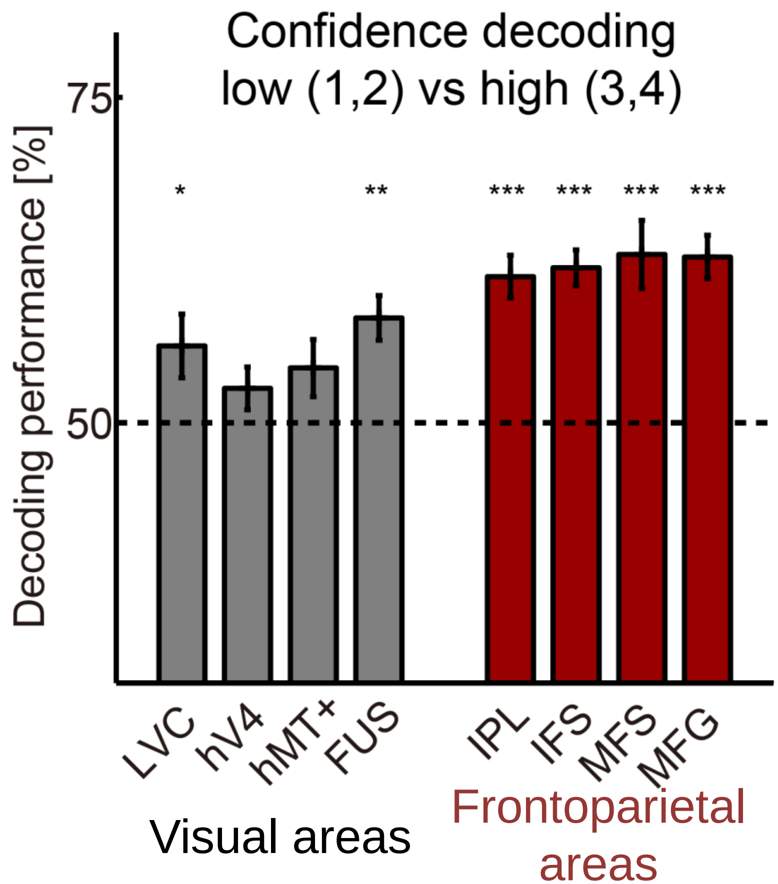
Confidence decoder construction



- Motion direction judgment
- Confidence rating of the motion direction judgment (1-4)

Confidence decoder was built from the activity
- in visual and frontoparietal areas
- during the coherent motion and delay periods

Confidence decoding from parietal and frontal areas

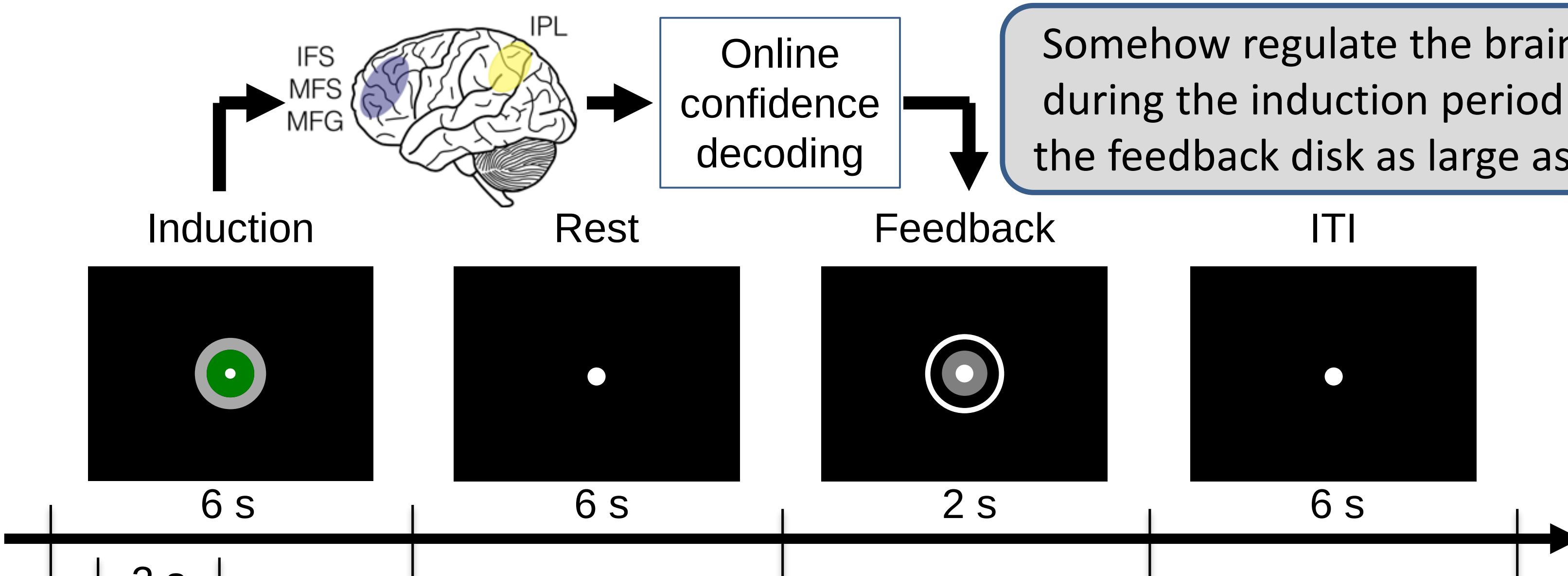


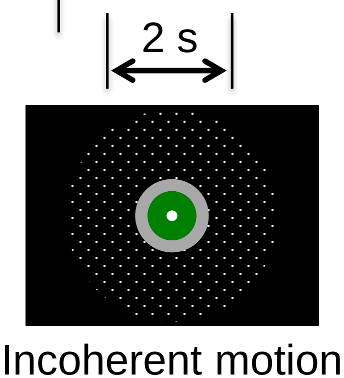
- Confidence decoded from the activity of parietal (IPL) and frontal (IFS, MFS, MFG) areas
- Confidence decoding accuracy was lower in visual areas

High/low confidence DecNef

Induction of activity patterns in the frontoparietal areas corresponding to high/low confidence

Somehow regulate the brain activity during the induction period to make the feedback disk as large as possible



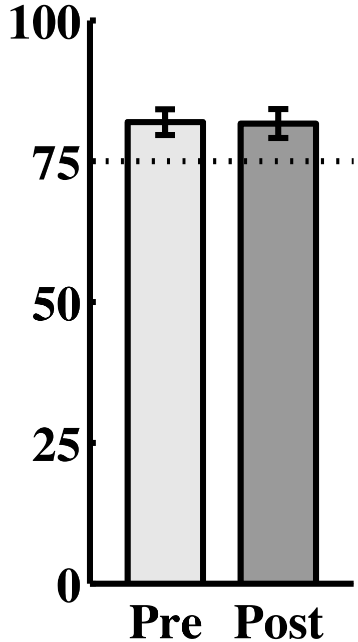


- Feedback disk size represents the similarity of frontoparietal activities between the induction period and the high or low confidence trials in the decoder construction
- Incoherent (random) motion was presented for 2 s at a random time during the induction period

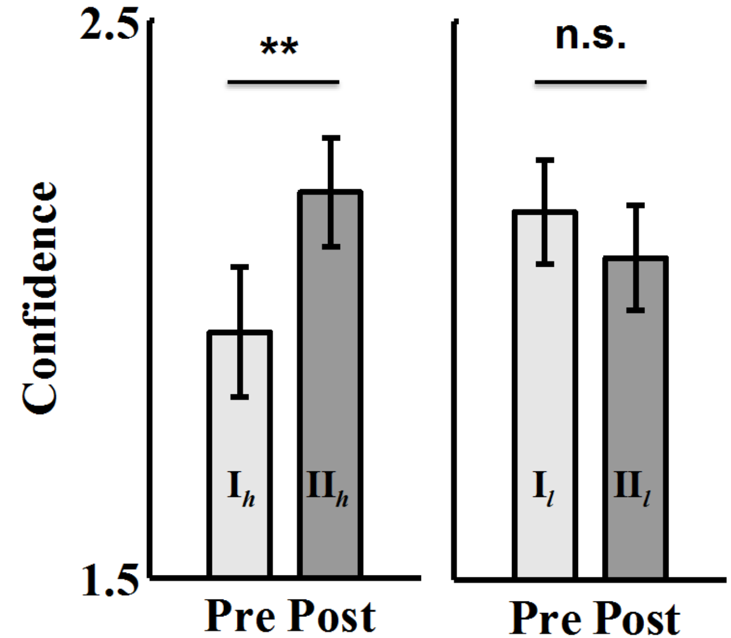
Before and after each DecNef session (high/low), direction discrimination accuracy and confidence were measured for the threshold level coherent motion

DecNef induced confidence changes
(without change in discrimination accuracy)

High-confidence DecNef | Low-confidence DecNef



High-confidence DecNef | Low-confidence DecNef



- No change in direction discrimination accuracy by DecNef (decoded neurofeedbck)
- Significant increase in confidence by high confidence DecNef

Conclusions

- Confidence was successfully decoded from fronto-parietal areas
- Induction of brain activities corresponding to high and low confidence resulted in the change in confidence rating without changing motion direction judgment accuracy
- Confidence is a rather separated entity from the other measures of perceptual accuracy

Fronto-parietal areas are causally related to confidence during the perceptual judgment

Overall summary

- Neural correlates of perception
  - Perceived jitter frequency mirrors intrinsic alpha frequency
- Decoded neurofeedback to study neural causes of perception
  - Long-lasting color perception associated with an orientation created by manipulation of V1/V2 activities
  - Change in confidence during direction judgment task achieved by manipulation of fronto-parietal activities

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Confidence DecNef

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