

Chapter 6 - Working Memory

BCSC

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THEME 6

WORKING MEMORY

Working memory는 actively¹하게 몇초간 기억을 유지하는 것.
Working memory는 의식적 기억을 지배하는 explicit memory.

working memory paradigms consist of a **study phase**, a **delay period**, and a **test phase**.

Working memory has been associated with activity in the **dorsolateral prefrontal cortex**, **the parietal cortex**, and **sensory processing regions**.
⇒ long-term memory와 유사한데, 해마 포함한 medial temporal lobe가 없어요!

6.1 The Contents of Working Memory

Working memory contents는 적극적으로 유지하는 모든 종류의 기억. e.g.,

- 머리에 맴도는 음악 한 소절에 취해
- 폰에 적기 전 뇌서 되새기고 있는 party 장소
- 복사기까지 가면서 시각화하고 있는 실험실 화이트 보드의 코드...??

working memory서 정보 유지?? ⇒ 오랜 기간 later sensory cortical regions 활성화! : fusiform face area(FFA) ㅇㅇ!!, V1 ㄴㄴ... V1은 later이 아님

++ claude왈, "Fusi-" = 라틴어 "fusus" (방추, spindle)

NOTE 6.1. 얼굴, 집, 공간 위치와 관련된 working memory 영역 찾는 fMRI 실험^a

¹actively는 의식적임을 뜻하나요? : Working memory refers to actively holding information in mind during a relatively short period of time, typically seconds.

Figure 6.1: On each trial, a cue instructed participants whether to maintain object (face or house) information or spatial location information during the working memory delay period. Items were presented during the sample/study phase, followed by the delay period, the test phase, and an inter-trial-interval (ITI) before the onset of the next trial (the time of each period, in seconds, is shown under each panel).

house identity, face identity, or spatial location에 대한 working memory를 시험함.

청사진:

- house identity, face identity, spatial location을 보여줌: 과제 제시
- 과제에 맞는 사진들을 보여주
- “Match” or “Non-match” button을 눌러주
- ITI 간격 기다리고 다시 실험해

e.g., ^b

House identity - “이 얼굴이 아까 본 얼굴 중 하나인가?”

- **Face identity** - “이 집이 아까 본 집 중 하나인가?”
- **Spatial location** - “이 위치가 아까 본 위치 중 하나인가?”

Figure 6.2: (B) Maintenance of faces during the delay period produced activity (in red/yellow) in the lateral fusiform cortex (i.e., the fusiform face area) and maintenance of houses during the delay period produced activity (in cyan/purple) in the medial fusiform/ parahippocampal cortex (i.e., the parahippocampal place area; axial view, occipital pole at the bottom). (C) Left, activity (percent signal change) in the superior dorsolateral prefrontal cortex (identified by contrasting working memory for spatial locations and control trials) was associated with maintenance of spatial locations (in green) to a greater degree than maintenance of faces (in red) and houses (in blue). Delay period activity corresponds to time points 2 to 4 (paradigm timing key at the top). Right, activity in the inferior dorsolateral prefrontal cortex (identified by contrasting working memory for faces and control trials) was associated with maintenance of faces (in red) and houses (in blue) to a greater degree than maintenance of spatial locations (in green).

delay동안 fMRI 측정 \Rightarrow face에 대하여는 house보다 lateral fusiform cortex(얼굴 인식과 관련)에서 더 강한 활성화 / 반대로, house에 대하여 face는 medial fusiform/parahippocampal cortex에서 더 강한 활성화

+ claude왈, “대비(contrast)”는 실험 조작이 아니라 데이터 분석 방법이에요! 각 조건의 뇌 활성화를 통계적으로 빼서 차이를 보는 거죠

또한 dorsolateral prefrontal cortex의 서로 다른 영역을 활성화

superior dorsolateral prefrontal cortex
working memory for spatial location과 더 큰 연관!

- inferior dorsolateral prefrontal cortex
working memory for faces and houses과 더 큰 관련!

pathway를 되세겨, dorsal 쪽은 where/spatial location processing, ventral 쪽은 what/identity processing하는 것과 일치함요

^a논문 링크 완전 길어

^b주의! 책 자세하지 못해 논문 gpt 돌렸음, 믿지 마셈요

6.1.1 dorsolateral prefrontal cortex

기존 지배적 의견: DL-PFC는 working memory의 contents를 저장하는 기본적인 장소임!

이거를 봐 — Figure 6.3 —, delay period 동안 활성화 되어 있는걸, V1 같은 early visual sensory regions와는 다르다구

Figure 6.3: Sustained working memory fMRI activity in the dorsolateral prefrontal cortex. Left, sustained activity (in gray/white) during the working memory delay period in the dorsolateral prefrontal cortex (the rightmost activation) and the parietal cortex (the leftmost activation; lateral view, occipital pole to the left). Right, working memory delay period activation timecourse (percent signal change as a function of time from study phase onset) extracted from the dorsolateral prefrontal cortex region within the white circle to the left. The delay period is illustrated by the gray bar.

새로운 의견: Curtis and D'Esposito (2003)왈, DL-PFC는 sensory cortical regions에 저장된 정보를 attention해주는 memory control processes해.

attention is all you neeeeeed??6.4

Figure 6.4: 놀라운 통찰력에 감명 받은 클로듀

NOTE 6.2. pattern classification algorithm을 사용한 V1 연구들

V1서 지속적인 working memory 관찰한 첫 fMRI 실험 http://www.psy.vanderbilt.edu/tonglab/web/papers/Harrison_Tong_Nature_2009.pdf

Figure 6.5: Timing of events for an example working memory trial. Two near-orthogonal gratings ($25 \pm 3^\circ$, $115 \pm 3^\circ$) were briefly presented in randomized order, followed by a numerical cue (green '1' or red '2') indicating which grating to remember. After an 11-s retention period, a test grating was presented, and subjects reported whether it was rotated clockwise or anti-clockwise relative to the cued grating.

11s의 delay period

~ 25° , ~ 115° 방향 격자(orientation grating)

이거 알려져 있기를 V1에 강한 자극: V1은 선 자극에 반응(!): 초기적

contrast ㄴ ㄴ! 대신: fMRI → voxel → multi-voxel pattern analysis and a pattern classification algorithm

pattern은 복잡해: with some voxels being positive in magnitude, some voxels being negative in magnitude, and some voxels having a magnitude of zero.

Figure 6.6: Orientation decoding results for areas V1–V4. The accuracy of orientation decoding for remembered gratings in the working memory experiment (green circles), unattended presentations of low-contrast gratings (red triangles), and generalization performance across the two experiments (black squares). Error bars indicate \pm s.e.m. Decoding was applied to the 120 most visually responsive voxels in each of V1, V2, V3 and V3A–V4 (480 voxels for V1–V4 pooled), as determined by their responses to a localizer stimulus ($1\text{--}4^\circ$ eccentricity). Individual areas V3A and V4 showed similar decoding performance but had fewer available voxels, so these regions were combined.

random? 50% 밖에 안 나옴, classification algorithm? 70%

V1 단순 현재 보는거 처리? ㄴ ㄴ, 기억까지 ㅇㅇ!

+ 유사한 실험 방법을 가진 다른 연구들,

V1 색상 정보도 유지,

V1과 V2 공간 정보도 유지: contralateral^a early visual regions는 우연보다 높음, 비단, ipsilateral early visual regions^b는 우연보다 높지 아니함. (chapter 1에서 비슷한 보고가 있었었??)

TMS를 활용한 연구

한쪽 반구의 V1 차단 → contralateral visual field의 working memory 능력 짜짜 저하: working memory 중 정확한 자극 표현 위해 V1 활성화 중요

요컨대, V1: 방향, 색, 공간 위치 지속적 유지

^a대측성, 반대편: 오른쪽 시야 → 왼쪽 뇌

^b동측성, 같은 편: 오른쪽 시야 → 오른쪽 뇌, 접두두사 ipsi: 자기 자신

contents of working memory? 아마 DL-PFC보다 sensory cortex이지

DL-PFC? sensory cortex? fMRI 시령 □

<https://pmc.ncbi.nlm.nih.gov/articles/PMC4379324/pdf/nihms-673125.pdf>

Figure 6.7: Behavioral task, BOLD timecourses, and anatomical regions of interest (ROIs). (A) Top: On each trial, participants were presented with two faces and two scenes and instructed to remember the relevant sample items (faces, scenes, or both faces and scenes). The sample images were immediately followed by a blank delay period, after which participants indicated whether the probe matched one of the relevant sample items. Bottom: Event-related BOLD timeseries were extracted from each of the ROIs, normalized, and averaged across participants. All error bars are s.e.m. The horizontal grayscale bar indicates the phase of the trial corresponding to BOLD and decoding measures, adjusted for the convolution with the hemodynamic response function.

실험 청사진:

- **study phase:** 2개의 얼굴과 2개의 집(? scenes)를 보여줌
→ 지시: 얼굴 기억해 / 집 기억해 / 둘다 기억해
- **delay period:** 9s

비교적 넓은 ROIs

- **Visual sensory regions:**
extrastriate cortical regions, the parahippocampal gyrus, and the fusiform gyrus (in both hemispheres)
- **Dorsolateral pre frontal regions:**
the middle frontal gyrus and the inferior frontal gyrus in both hemispheres

study phase에서는 DL-PFC 활성화 큰데, delay는 아냐 ⇒ 일단 DL-PFC는 working memory 저장소 아닐듯?

저자들의 가정: working memory를 저장하는 영역은 의미있는 활동 패턴을 가진다:
→ 집은 얼굴 보다 얼굴/집에 더 유사, 마찬가지로 얼굴은 집보다 얼굴/집에 더 유사

실험 방법: 또 classifier 만들어: 집, 얼굴, 집/얼굴 3가지로 분류

Figure 6.8: To distinguish between the storage of a sensory representation versus a non-sensory representation, we examined the misclassification of Remember Faces and Remember Scenes trials during the delay period. The classifier was disproportionately more likely to incorrectly guess Remember Both than the opposite category (i.e., guess Remember Faces on Remember Scenes trials and vice versa) in EC, consistent with a sensory representation, but not in lPFC. * indicates $p \leq 0.0001$.

Proportion of Classifier Guesses: (특정 유형의 틀린 답 개수) / (전체 틀린 답 개수)
→ 가정에 따라 sensory cortex가 working memory의 저장소인듯?
문제는 가정에서 시작함.

DL-PFC에 working memory가 저장된다는 것은 배타적인 이론. 더 많은 연구 부탁드림

6.2 Working Memory and the Hippocampus

해마: long-term memory인 episodic memory와 item memory와 관련되어 있어

그는 일생 동안 사생활 보호를 위해 H.M.으로 세상에 알려져 있었다. 수많은 의사와 과학자들이 그를 연구하면서 H.M.은 브로카의 환자 탄 이후에 가장 유명한 신경심리학의 연구 사례가 되었다. 1953년 27세의 H.M.의 간질이 내측 측두엽^{MTL}에서 발생했다고 생각하고, H.M.의 뇌 양쪽에서 이 영역들을 제거했다. 수술 후에 H.M.은 정상 같이 보였다. 그의 인성, 지성, 운동 능력 그리고 유머 감각에는 전혀 손상이 없었다. 남은 일생 동안 그는 자신이 왜 그곳에 있는지를 전혀 기억하지 못한 채 매일 아침 병실에서 일어났다. 매일 만나는 간병인들의 이름도 익힐 수 없었다. 그는 대통령의 이름도 몰랐고, 현재의 사건들을 설명할 수도 없었다. 반면에 H.M.은 수술 이전에 일어났던 일들은 여전히 기억하고 있었다. 내측측두엽은 새로운 기억을 저장하는 데 핵심적이지만 오래된 기억을 유지하는 데는 중요하지 않은 것으로 보였다. 앞에서 언급했듯이 이차크 프리드와 그의 동료들은 내측 측두엽에서 제니퍼 애니스톤 뉴런과 할리 베리 뉴런을 발견했으며, 이 영역이 지각과 생각 모두에 관련되어 있음을 확인했다. 이후...

– H.M.의 이야기

수술 이전에 일어났던 일들은 여전히 기억하고 있었다?

환자 H.M.: working memory는 존재! → 해마와 working memory는 관련 없나?

최근 연구 알, working memory: long-term memory처럼 해마와 관련될 수도?? 실험을 살펴 보아

Hannula Ranganath, 2008^a

Figure 6.9: A, Illustration of the events associated with a single short-term memory trial. B, Examples of the three types of test displays; test displays were always rotated 90° counter-clockwise relative to the sample. Object-location bindings were intact in match displays, one of the objects (drums) moved to a new, previously unoccupied, location in mismatch-position displays, and two of the objects (drums, birdbath) swapped positions in mismatch-swap displays.

청사진:

- **study phase:** 4개 물체 보여줌, 격자에 있음
- **delay phase:** 11초, 90° 회전된 모습을 생각해
- **test phase:** 상상과 일치하는지 여부 대답해

맞, 아니 맞 대비:

- study phase: 해마 차이
- delay phase: 해마 차이 아님
- test phase: 해마 차이

⇒ 저자 왈, study phase, test phase 해마 차이는 working memory가 해마와 관련되어 있다는 증거!

? CN 이의

- working memory와 실질적 관련된 부분은 delay phase, 차이 없어
- s, t서 새로운 자극 → 해마 활성화
- 공간 처리와 큰 관련 → 해마!
- 마도, s, t서 term memory encoding processes 발생?

나: working memory, STM 같은거로 치부 가능??

^a<https://pmc.ncbi.nlm.nih.gov/articles/PMC2748793/pdf/zns116.pdf>

Bergmann, Rijpkema, Fernández Kessels, 2012^a

Figure 6.10: Schematic overview of the delayed-match-to-sample-task (a) and the two long-term memory tasks (b and c). Panel (a) shows a schematic representation of one trial of the delayed-match-to-sample task (with high-arousal stimuli).

청사진:

- study phase: 4개의 얼굴, 집(!) 쌍 보여줌
- delay phase: 10s
- test phase: 3개, 동일? 재배열?
- surprise!: 갑작스러운 테스트

맞춘 것도 long-term memory와 working memory로 나눌 수 있어,
해마는 working memory ㄴ ㄴ, long-term memory ㅇ ㅇ!

^a<https://pmc.ncbi.nlm.nih.gov/articles/PMC3530455/pdf/pone.0052616.pdf>

⇒ 해마와 working memory 관계 말해주는 fMRI 증거 ㄴ ㄴ

brain lesion 실험도 관계 찾고파

(Finke et al., 2008)^a

Figure 6.11: Color and/or location working memory paradigms and medial temporal lobe lesion results. (A) During each color working memory trial, illustrated at the top, colored squares were presented during the sample/study phase, there was a 900- or 5000- millisecond delay period, and then there was a probe/test phase in which participants made “match”–“non-match” judgments. The same paradigm was used for location and association (i.e., color and location) trials, illustrated at the middle and bottom, respectively. (B) Performance (percent correct) on the color, location, and association working memory tasks as a function of delay period duration (in milliseconds) for patients with medial temporal lobe damage and control participants that did not have a brain lesion (asterisks indicate significantly impaired performance in the patients as compared to control participants).

피험자: right medial temporal lobe 제거된 3명

delay: 900ms/500ms

5000ms, association에서 환자와 차이 커

저자왈, association 관련 working memory와 해마 관계있는 듯

CN 이의:

- working memory면 900ms도 문제 있어야, 5000ms long-term memory 과정인듯?
- 공간처리는 해마짜짜냐
- lesion이 해마만이 아냐, the right amygdala, the hippocampus, the entorhinal cortex, and the perirhinal cortex

^a<https://pubmed.ncbi.nlm.nih.gov/18705734/>

후속 연구:

- Baddeley, Allen Vargha-Khadem, 2010 해마만 손상된 환자
- (Allen, Vargha-Khadem Baddeley, 2014 동일 환자로 공간 시험 빼고
⇒ 해마와 관련 없는 듯?
H.M. 사례 맞는 듯?

6.3 Working Memory and Brain Frequencies

working memory 관련 frequency band:

- theta frequency band (4 to 8 Hertz)
- alpha frequency band (8 to 12 Hertz)
- gamma frequency band (greater than 30 Hertz)

long-term memory 처럼... alpha: inhibition, gamma: binding of information in different cortical regions

long-term memory: theta - 해마-피질 상호작용, working memory에서는 ????

Sauseng et al., 2009

theta activity, alpha activity, and gamma activity during working memory가 궁금해

Figure 6.12: Color working memory paradigm and EEG results. (A) During each trial, an arrow cued one hemifield. The memory array/study phase consisted of two to six(???) colored squares in each hemifield, followed by a retention interval/delay period where the stimuli in the cued hemifield were maintained, and then during the probe/test phase participants indicated whether or not any of the colors in the cued hemifield had changed. (B) Left, theta-gamma synchronization as a function of the number of items in working memory (i.e., working memory load) at contralateral and ipsilateral occipital-parietal recording sites (key to the right). Right, alpha activity as a function of working memory load at contralateral and ipsilateral occipital-parietal recording sites.

청사진:

- 주의할 곳 화살표로 표시
- 2-6개 색 있는 사각형
- delay
- 바뀌었음??

6.4 Brain Plasticity and Working Memory Training

DEFINITION 6.1. brain plasticity working memory 훈련이 뇌 활동을 변화시키는 것을 brain plasticity라고 한다.

⇒ working memory 과제 계속해! → improves performance on that task, improve intelligence(!!!)

NOTE 6.3. Jolles, Grol, Van Buchem, Rombouts Crone, 2010 <https://www.sciencedirect.com/science/article/pii/S1053811910004234?via%3Dihub>

3-5개 물건 순차적 제시→기억해/역순으로 기억해→1개 보여주고 물체 순서 버튼 눌러

주 3회 25분씩, 6주 연습

연습 전(timepoint 1), 연습 후(timepoint 2), 일부 6개월 또 후(timepoint 3)

Figure 6.13: Behavioral effects and brain effects of working memory training. (A) Working memory accuracy (percent correct) as a function of time (time point 1 = pre-training, time point 2 = 6 weeks of training, time point 3 = 6 months after time point 2) and load (key at the bottom right). (B) fMRI activity (in dark gray) at time point 2 versus time point 1 (axial view, occipital pole at the bottom).

improve with training, particularly for higher working memory loads of four or five items, and these improvements were sustained 6 months after training

the anterior prefrontal cortex and the parietal cortex 활동 업/다운 동시→ 모순적? 아니아니, 넓은 지역, 여러 기능

활동 늘어난 것은 관련시키는 능력 chunking과 attention 유발 포함

- 장기 훈련:
활동 증가/감소 모두
- 단기 훈련(1시간 미만):
감소, visual sensory regions도 감소: repetition priming(최적의, 더 적은 energy)

→ 새로운 전략, 효율적인 network 만드는데 시간 걸려

increase in behavioral performance: dorsolateral prefrontal cortex and the parietal cortex→ working memory, long-term memory, imagery, and attention 등에 영향
working memory는 혹시 imagery의 단순히 다른 표현???